HEREDITAS

GENETISKT ARKIV

UTGIVET AV MENDELSKA SÄLLSKAPET I LUND

REDAKTÖR: ROBERT LARSSON

BAND XXIV 1938

LUND 1938, BERLINGSKA BOKTRYCKERIET

ZYTOLOGISCHE STUDIEN AN SALIX-BASTARDEN

VON *ARTUR HÅKANSSON*

LUND

(With a Summary in English)

WÄHREND längerer Zeit habe ich Material der zahlreichen *Salix*-Formen und -Bastarde fixiert, die Professor HERIBERT NILSSON in Lund in Kultur gehabt hat. Teils sind Wurzelspitzen fixiert worden, die man von vielen — aber bei weitem nicht von allen — leicht durch Einsetzen von abgeschnittenen Zweigen in Wasser erhalten kann. Man könnte glauben, dass es also im allgemeinen leicht sein sollte die somatische Chromosomenzahl zu bestimmen, aber leider ist dies nicht der Fall. Von verschiedenen Typen, und gerade von einigen die mich am meisten interessierten, war es unmöglich vollgute Fixierungen zu bekommen. Teils sind Staubgefässe und Fruchtknoten fixiert worden um die Meiosis, besonders die Chromosomenpaarung in Metaphase 1 zu studieren. Recht zeitraubend ist eine Untersuchung der Embryosackmutterzelle, die aber häufig unvermeidlich ist, da in den meisten Fällen weibliche Sträucher unter den Bastarden dominieren und von manchen Kreuzungen ausschliesslich weibliche Sträucher erhalten worden sind (z. B. von den *cinerea*-Bastarden im allgemeinen).

Von meinen Studien ist früher ein Teil veröffentlicht worden, nämlich über die Kreuzung *S. viminalis* × *caprea* (HÅKANSSON, 1929), ferner über die Bastarde *S. nigricans* × *phylicifolia* — also ein Bastard zwischen zwei hexaploiden Arten — sowie über *S.* (*nigricans* × *phylicifolia*) × (*viminalis* × *caprea*), also eine Kreuzung zwischen einem hexaploiden und einem diploiden Bastard (HÅKANSSON, 1933). Die Grundzahl für die Chromosomen in der Gattung *Salix* beträgt bekanntlich 19. Sämtliche diese Bastarde haben eine sehr regelmässige Meiosis. In der vorliegenden Untersuchung sollen einige Ergänzungen zu früheren Beobachtungen über den Bastard *viminalis* × *caprea* sowie Beschreibungen einiger neuen Bastarde mitgeteilt werden. Sämtliche sind von Professor HERIBERT NILSSON dargestellt, der auch einige präliminäre Angaben über gefundene Chromosomenzahlen gemacht hat.

Es sind verschiedene Fixierungsmittel verwendet worden und die besten Resultate sind mit BOUIN-ALLEN nach Vorfixierung mit CARNOY

erhalten worden. Die Färbung der Präparate geschah meistens mit Gentianaviolett, zuweilen jedoch mit Hämatoxylin nach HEIDENHAIN.

SALIX VIMINALIS × CAPREA, F_2.

Triploide Sträucher. — Die Meiosis verläuft beim F_1-Bastarden, wie früher konstatiert worden ist, sehr regelmässig wie bei den reinen Arten. Es bestand jedoch eine Neigung Pollenkörner mit der diploiden Chromosomenzahl zu bilden, was auf Störungen beruhte, die während der zweiten Teilung eintrafen. Diese Störungen hatten auch Folgen. In der F_2-Generation gab es zwei Sträucher mit abweichender Chromosomenzahl. Es gab einen triploiden, männlichen Strauch mit sehr grossen Blättern und kräftigem Wuchs, daher *gigantea* genannt, und ferner einen Strauch mit mehr als der tetraploiden Chromosomenzahl (vielleicht war er pentaploid), der ganz der bekannten Gartenform *S. laurina* glich.

Weitere Untersuchungen haben gezeigt, dass triploide Sträucher in F_2 nicht selten sind. Neue solche sind teils in der alten Kreuzung, teils in einer später dargestellten gefunden worden. Es scheint, als ob wenigstens 1 % der F_2-Sträucher triploid seien, dies trotz der regelmässigen Reduktionsteilung in F_1. In der alten Kreuzung gab es noch einen triploiden, männlichen Strauch. Dieser hatte ein ganz anderes Aussehen als die anderen Triploiden und war nicht vom *gigantea*-Typus. Er hat schmale sichelförmige Blätter (siehe HERIBERT NILSSON, 1918) und ist *falcifolia* genannt worden. In der neuen Kreuzung sind fünf Triploide festgestellt worden, aber wahrscheinlich gibt es mehr solche, da einige Sträucher vom *gigantea*-Typus noch nicht untersucht worden sind. Von den Triploiden waren drei männlich und zwei weiblich, die ersten die gefunden worden sind. Eine Intersexualität bei den Triploiden, die bei *Rumex acetosa* häufig ist, wurde hier nicht beobachtet.

Die Chromosomen sind im allgemeinen sowohl in Wurzelspitzen wie während der Meiosis studiert worden. In der früher veröffentlichten Arbeit ist die Meiosis in einem triploiden ♂-*Salix*-Strauch ausführlich geschildert worden. Charakteristisch war eine ausgeprägte Tendenz Trivalente zu bilden, in Extremfällen gab es 19 solche. Ferner zeigte der Beginn der Anaphase 1 starke Unregelmässigkeiten, da mehrere Chromosomen verspätet und zuweilen univalente Chromosomen längsgeteilt wurden. Die später gefundenen ♂-Triploiden zeigten eine ähnliche Meiosis (Fig. 1 *a*).

Die Meiosis der ♀-Sträucher wurde auch durch das Vorkommen

von Trivalenten in der Metaphase 1 charakterisiert. Die Anzahl von Trivalenten schien jedoch im allgemeinen geringer zu sein als in den Pollenmutterzellen. Es stiess auf allzu grosse Schwierigkeiten ein genügend grosses Material zu erhalten um diese Erscheinung sicher beweisen zu können, aber in den untersuchten Zellen war die Anzahl gering, etwa 7 (Fig. 1 *b*), während bei den ♂-Sträuchern etwa doppelt soviele häufig sind. Dass die Paarungsverhältnisse in der Metaphase 1

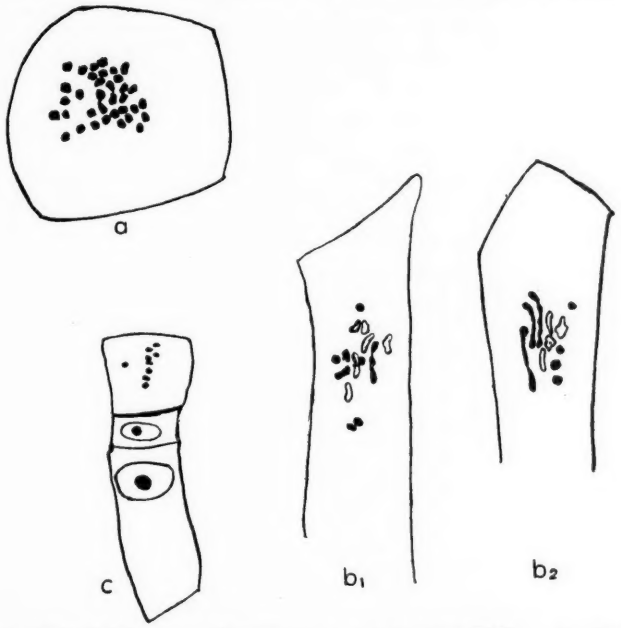


Fig. 1. *S. viminalis* × *caprea, gigantea.* — *a*: A 1 in einer PMZ. — b_1—b_2: M 1 in einer EMZ. Alle beobachteten Chromosomen sind nicht eingezeichnet, die Bivalente nur im Umriss. — *c*: Die Teilung der mikropylaren Diadenzelle ist verspätet.

bei ♂- und ♀-Individuen des gleichen Bastards verschieden sind, ist früher in mehreren Fällen nachgewiesen worden, so im Schmetterlingsbastard *Pygœra pigra* × *curtula.* Die Weibchen zeigen bei diesem eine fast vollständige Chromosomenpaarung, während sie bei den Männchen aufgehoben ist (FEDERLEY, 1931).

Wie später mitgeteilt werden soll, ist die Meiosis bei mehreren triploiden Artbastarden in der Embryosackmutterzelle stark verspätet. Dies ist jedoch bei triploiden *viminalis* × *caprea* nicht der Fall, eine beträchtlichere Verspätung im Vergleich mit dem diploiden Bastarden

ist hier nicht festzustellen. Die Teilungen finden im allgemeinen statt, wenn das Integument über den Nuzellus hinaufwächst oder zu einem Mikropylarkanal zusammenwächst. Die Entwicklung des Embryosackes erfolgt nach dem Normaltypus, und der achtkernige Embryosack verdrängt die Epidermiszellen im Scheitel des Nuzellus. Häufig wird die mikropylare Diadenzelle verspätet geteilt, und die Teilung ist mitunter von Chromosomenstörungen begleitet (Fig. 1 *c*).

In vielen Samenanlagen kommt es zu Degeneration, es wird kein Embryosack ausgebildet. Etwa $^2/_3$ der fertigen Samenanlagen sind leer. Dies beruht jedoch nicht auf einer ausgebliebenen Teilung der Embryosackmutterzelle. Diese wird fast immer geteilt, und die Degeneration erfolgt *nach* der Teilung. Sehr häufig wurden zwei tote Diadenzellen im Nuzellus beobachtet, die Entwicklung ist nicht bis zur zweiten Teilung gekommen. In anderen Samenanlagen degeneriert die Makrosporentetrade. Dass also die Degeneration nach und nicht vor der Reduktion eintrifft, deutet darauf hin, dass sie durch eine ungeeignete Kombination von Chromosomen oder ungeeigneter Anzahl verursacht wird.

Die Entstehung von triploiden männlichen Sträuchern ist früher erörtert worden (HÅKANSSON, 1929). Ein triploider weiblicher Strauch soll ja entstehen, wenn eine diploide (unreduzierte) Eizelle im F_1-Bastard von einer haploiden männlichen Gamete befruchtet wird. Aber wahrscheinlich kann sie auch aus einer haploiden Eizelle gebildet werden, wenn die befruchtende diploide männliche Gamete infolge einer Chromosomenverdoppelung nach der Reduktion entstanden ist, also eine XX-Gamete darstellt. Das abweichende Aussehen von *S. falcifolia* deutet darauf, dass dieser ♂-Strauch seine Entstehung einer Verdoppelung zu verdanken hat, die nach Umkombination der Chromosomen durch die Reduktionsteilung erfolgt ist.

Ein tetraploider Strauch. — In der F_2-Generation der neuen Kreuzung *S. viminalis* × *caprea* gab es einen weiblichen Strauch, der *S. cinerea* sehr ähnlich war. Er stimmte mit dieser Art »in bezug auf alle wichtigen taxonomischen Merkmale» überein. »Sie (die Form) kann also mit Recht *S. neocinerea* genannt werden. Denn in der Natur gefunden, wäre sie ohne geringsten Zweifel in *S. cinerea* eingereiht worden.» (HERIBERT NILSSON, 1931, S. 315). HERIBERT NILSSON gibt auch an, dass der Strauch eine höhere als die diploide Chromosomenzahl hatte, er war wenigstens triploid, und dass er »also auch in dieser Hinsicht von den Eltern abweicht und sich *cinerea* nähert» (l. c. S. 316).

Ein eingehendes Studium von *S. neocinerea* zeigt indessen, dass sie

gleichwie *cinerea* tetraploid ist. Es zeigte sich, dass das Feststellen der Chromosomenzahl in den Kernplatten in Wurzelspitzen recht schwierig war, in keiner konnten 76 Chromosomen gezählt werden; Fig. 2 *a* zeigt 73. Wie indessen aus der Reduktionsteilung hervorgeht, besteht kein Zweifel darüber, dass die somatische Chromosomenzahl 76 ist, also der tetraploiden Zahl entspricht.

Die Meiosis in der Embryosackmutterzelle trifft ein, wenn das Integument über den Nuzellus hinaufwächst oder sich zum Mikropylarkanal zusammenschliesst, also im gleichen Stadium der Entwicklung des Fruchtknotens wie bei fertilen *Salices*. Die Chromosomenpaarung in der Metaphase 1 war von gewissem Interesse. Zufolge des ziemlich hohen Prozentes von Trivalenten bei den triploiden Sträuchern erwartete man, dass bei den Tetraploiden Quadrivalente vorkommen sollten. Dies war jedoch meistens nicht der Fall. In der Metaphase 1 gab es entweder nur Bivalente oder auch nur einzelne Multivalente. Fig. 2 *c* zeigte eine Metaphase 1 vom Pol aus gesehen; in dieser Zelle gibt es zweifellos 36 Bivalente und 1 Quadrivalent. In Fig. 2 *b* sind nur einige Chromosomen von einer Zelle mit ausschliesslich Bivalenten abgebildet. Diese liegen nicht alle genau in der Äquatorialebene sondern in etwas verschiedener Höhe, was bei dieser Form recht häufig ist. Fig. 2 *d* zeigt die Chromosomen von einer Metaphase 1. In dieser Zelle war die Multivalentbildung verhältnismässig ausgesprochen, indem man deutlich 1 Quadrivalent, 2 Trivalente, aber sonst nur Bivalente unterscheiden konnte. Es gelang nicht alle Bivalente zu zählen, was in den längsgeschnittenen Metaphasen sehr schwierig ist, aber die Paarung in dieser Zelle dürfte keine grössere Anzahl Multivalente hervorgebracht haben als abgebildet sind. Die Anaphase 1 war regelmässig, zuweilen war ein Chromosom verzögert, vermutlich als Folge von Multivalentbildung (Fig. 2 *e*).

Die zweite Teilung war regelmässig. Eine Kernplatte von der mikropylaren Diadenzelle ist in Fig. 2 *g* abgebildet. Sie hat 38 Chromosomen. Fig. 2 *h* zeigt die Telophase 2. Gewöhnlich liegen die vier Makrosporen in einer Reihe oder in T-Form. Aber mitunter wird die chalazale Diadenzelle durch eine längsgehende Wand geteilt (Fig. 2 *f*). Eine Längsteilung dieser Zelle ist eine seltene Erscheinung unter den Angiospermen. Bei mehreren *Salix*-Kombinationen wird jedoch die chalazale Diadenzelle recht häufig longitudinal geteilt, so bei *S. laurina*, und den meisten Bastarden, die *S. cinerea* enthalten. Die weitere Entwicklung scheint keine Eigentümlichkeiten aufzuweisen. In den meisten Samenanlagen wird ein Embryosack von normalem Aussehen ge-

bildet, der sicherlich vollkommen fertil ist. HERIBERT NILSSON hat auch nach Pollination mit *S. cinerea* guten Samenansatz gefunden, dagegen nicht nach Pollination mit den Elternarten (laut freundlicher Mitteilung).

S. neocinerea ist also nicht nur phänotypisch *S. cinerea* ähnlich, sondern stimmt auch zytologisch mit dieser Art überein und bildet nor-

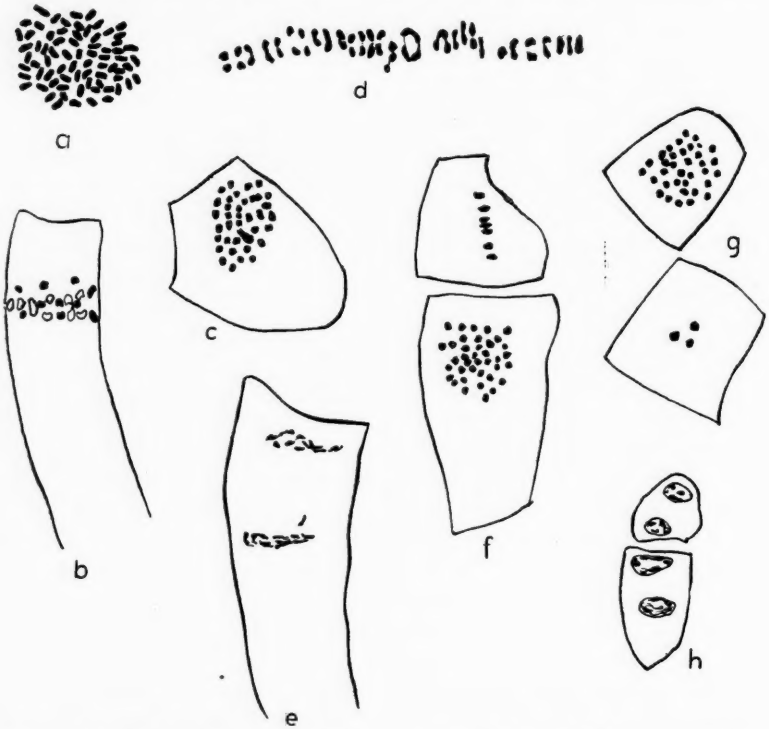


Fig. 2. *S. viminalis* × *caprea, neocinerea.* — *a*: Somatische Kernplatte. — *b*: M 1 in der EMZ. — *c*: M 1 quergeschnitten, $36_{II} + 1_{IV}$. — *d*: Die Chromosomen in M 1, $1_{IV} + 2_{III}$, sonst II-en. — *e*: Späte A 1. — *f*: M 2. — *g*: M 2. — *h*: T 2.

male fertile Embryosäcke aus. Dies bestätigt die von HERIBERT NILSSON hervorgehobene Ansicht, dass sie einen Parallelfall zu MÜNTZINGS bekannter synthetischer *Galeopsis Tetrahit* darstelle (MÜNTZING, 1930, S. 318). Diese entstand ja in der Weise, dass in der F_2-Generation einer Kreuzung zwischen den beiden diploiden Arten *G. pubescens* und *speciosa* eine triploide Pflanze auftrat. Diese wurde mit *pubescens* gekreuzt

und gab als Resultat den tetraploiden Typus. MÜNTZING hat wahrscheinlich gemacht, dass letztere zwei *pubescens*-Genome, ein *speciosa*-Genom und ein Rekombinationsgenom enthält, da die Triploide ein *pubescens*-, ein *speciosa*- und ein Rekombinationsgenom enthalten haben sollte (MÜNTZING, 1932).

S. neocinerea ist direkt aus dem diploiden Bastard ohne Vermittlung über eine Triploide entstanden. Dies erschwert in hohem Grade die Erörterung seiner Entstehung und seiner Genomzusammensetzung. Denn offenbar gibt es mehrere verschiedene Arten von Erklärung dieser Form. Sie kann aus einer unreduzierten männlichen Gamete und einer unreduzierten weiblichen Gamete entstanden sein, in welchem Falle sie zwei *viminalis*- und zwei *caprea*-Genome enthalten sollte. Solche Gameten werden ja offenbar in nicht allzu unbedeutender Anzahl gebildet (zytologisch jedoch in den weiblichen Sträuchern nicht nachgewiesen), und die Möglichkeit dass zwei solche zusammentreffen ist vorhanden. Es scheint mir jedoch, dass *neocinerea* ein so abweichendes Aussehen hat, dass sie kaum auf diese Weise entstanden sein kann. Mit dieser Genomzusammensetzung sollte sie wohl am ehesten wie ein extremer *gigantea*-Typus ausgesehen haben. Das Zutagetreten verschiedener *cinerea*-Eigenschaften deutet eher darauf hin, dass die Chromosomenverdoppelung nach Rekombination der Chromosomen durch die Reduktionsteilung stattgefunden hat, sodass *neocinerea* entweder ausschliesslich Rekombinationsgenome oder solche und überdies reine Artgenome enthalten sollte.

Wie früher erwähnt worden ist, gibt es zytologische Indizien dafür, dass diploide Pollenkörner auch zufolge einer Chromosomenverdoppelung nach der Reduktion gebildet werden können (siehe oben und ferner HÅKANSSON, 1929, S. 7). Die Gameten werden also zwei identische Rekombinationsgenome enthalten und könnten eine diploide weibliche Gamete befruchten, entweder eine unreduzierte solche mit einem *viminalis*- und einem *caprea*-Genom, oder auch eine diploide weibliche Gamete, die in gleicher Weise wie die männliche Gamete entstanden ist, also mit zwei identischen Rekombinationsgenomen. Das Letztgenannte ist natürlich keine besonders wahrscheinliche Bildungsweise für *neocinerea*. Die Möglichkeit der Verschmelzung einer triploiden männlichen Gamete und einer haploiden weiblichen besteht zweifellos auch; man könnte sich da vorstellen, dass drei Pollentetradenkerne vereinigt worden sind, beim diploiden Bastarden ist dies nicht beobachtet worden, dagegen einmal bei *gigantea*. Schliesslich gibt es eine weitere Möglichkeit für die Entstehung von *neocinerea*, nämlich dass keine

Verschmelzung von Gameten mit abweichender Chromosomenzahl stattgefunden hat, sondern eine gewöhnliche Befruchtung, dass aber bei der ersten Teilung der Eizelle oder im jungen Embryo eine Chromosomenverdoppelung stattgefunden hat. Experimentell hat man tetraploide Maispflanzen durch Wärmebehandlung zur Zeit der Befruchtung erhalten (RANDOLPH, 1932). Dass in diesem Stadium eine Chromosomenverdoppelung erfolgen kann ist also nachgewiesen, und es besteht vielleicht die Möglichkeit, dass sie spontan ohne veränderte äussere Faktoren eintreffen kann. Eine derartige Bildungsweise würde eine Tetraploide mit zwei verdoppelten Rekombinationsgenomen geben.

Der geringe Grad von Multivalentbildung bei *neocinerea* verglichen mit der grossen Anzahl von Trivalenten bei den triploiden Sträuchern hat ein Gegenstück bei ein paar anderen experimentell dargestellten Polyploiden. Ein triploides *Solanum nigrum* besitzt Trivalente, das tetraploide trotzdem nur Bivalente (laut JÖRGENSEN, 1928). Ein synthetisches *Galeopsis Tetrahit* hat nur Bivalente, obgleich die triploide Form nicht selten Trivalente bildet und das diploide *G. pubescens* × *speciosa* häufig vollständige Paarung zeigt (MÜNTZING, 1932). Literaturübersichten in dieser Frage sind vom letztgenannten Forscher mitgeteilt worden (MÜNTZING, 1936, 1937). Man ist der Ansicht, dass die geschwächte Quadrivalentbildung auf geringer Chiasmafrequenz und unbedeutender Chromosomengrösse beruht. Die *Salix*-Chromosomen haben diese Eigenschaften. Dass, wie erwähnt worden ist, *neocinerea* nicht mit den Eltern gekreuzt werden kann, beruht auf der veränderten Chromosomenzahl. Es gibt mehrere Beispiele dafür, dass Tetraploide gar keine oder mit der grössten Schwierigkeit Bastarde mit den entsprechenden Diploiden geben.

Seit dem Jahre 1927 hat man zwischen Autopolyploiden, die dasselbe Genom mehrmals besitzen, und Allopolyploiden unterschieden, die verschiedene Genome enthalten. Nunmehr erscheint die Grenze zwischen diesen beiden nicht mehr so scharf. Es ist hervorgehoben worden, dass als Autopolyploidie Fälle zu betrachten sind, in denen Genome vereinigt sind, deren Chromosomen homolog sind, auch wenn sie in bezug auf die Gene heterozygotisch sind (LILIENFELD, 1936). MÜNTZING (1936) definiert auch Autopolyploide als Polyploide, deren Genome strukturell gleich sind. Laut dieser Auffassung sollen die polyploiden Sträucher der *S. viminalis* × *caprea*-Kreuzung Auto-Typus haben, obgleich die beiden Elternarten sehr verschieden sind. Strukturelle Unterschiede haben nicht konstatiert werden können; sie sollten ja in der

Meiosis des F_1-Bastarden zutage getreten sein. Mit Hinblick auf die Chromosomen sind sie also Autopolyploide, mit Hinblick auf die Entstehungsweise interspezifische Polyploide (FAGERLIND, 1937).

SALIX VIMINALIS × (VIMINALIS × CAPREA, TRIPLOID).

Die untersuchten Sträucher wurden mittels Pollen von der in einer früheren Arbeit zytologisch beschriebenen Triploide 528 erhalten (HÅKANSSON, 1929). Sie sind demnach das Resultat einer Rückkreuzung der Triploide mit einer der Elternarten (2X × 3X). Die Serie enthielt nur eine geringere Anzahl Sträucher, und Fixierungen wurden teils von den Ähren, teils von auswachsenden Wurzeln gemacht.

Sechs Sträucher sind untersucht worden, zwei weibliche und vier männliche. Der eine der beiden weiblichen Sträucher war diploid, der andere triploid. Der erste war ein sehr stark wachsender Strauch, grösser als alle Geschwister. Man könnte Tetraploidie vermuten, aber die Metaphase 1 zeigte 19 Bivalente und in den Wurzelspitzen gab es 38 Chromosomen. Auch die Chromosomen des triploiden Strauches wurden sowohl in Wurzelspitzen wie in Embryosackmutterzellen studiert. Die somatischen Zellen hatten zweifellos 57 Chromosomen; während der Meiosis konnte die Chromosomenzahl nicht exakt bestimmt werden, aber sie verlief wie bei den früher beschriebenen triploiden weiblichen Sträuchern. In der Metaphase 1 gab es tri-, bi- und univalente Chromosomen, die Anaphase 1 war sehr unregelmässig (Fig. 3 *a*).

Von den vier männlichen Sträuchern war einer diploid, zwei triploid und einer aneuploid. Die Chromosomenzahl des diploiden und eines der triploiden Sträucher wurde nach einem Studium von Wurzelspitzen bestimmt. Die Chromosomen des zweiten triploiden Strauches konnten nur in den Pollenmutterzellen studiert werden, da keine Wurzeln erhalten wurden. Man kann daher nicht mit Bestimmtheit sagen, dass die Chromosomenzahl 57 betrug, aber sie lag sicher nahe dieser Zahl; die Meiosis war nämlich ganz wie bei 528 mit nur wenigen Univalenten, dagegen mit vielen Trivalenten in Metaphase 1, während man in Anaphase 1 in vorteilhaften Kernplatten 25—28 Chromosomen zählen konnte. Schliesslich gab es einen mit Sicherheit aneuploiden Strauch. In Wurzelzellen dieses wurden 41 Chromosomen gezählt (Fig. 3 *b*). Die Meiosis war ziemlich schwer zu studieren. Die Metaphase 1 hatte ein oder einige wenige Trivalente, im übrigen Bivalente (Fig. 3 *c*), zuweilen sah man ein Univalent. Zu Beginn von Ana-

phase 1 konnte man zurückgebliebene Chromosomen beobachten, eine häufige Erscheinung bei *Salix*-Formen mit Trivalent- oder Univalentbildung (Fig. 3 *d*). Die zweite Teilung verlief häufig regelmässig, zurückgebliebene Chromosomen sah man aber oft (Fig. 3 *e*). Es ist dies der erste aneuploide Strauch, den ich bei *Salix* sicher habe konstatieren können (*S. laurina* vielleicht ausgenommen).

Es gab also zwei Sträucher mit 38, einen mit 41 und drei mit 57 Chromosomen. Dies bedeutet eine sehr starke Selektion. Die Meiosis in 528 war sehr unregelmässig, Elimination von Chromosomen war

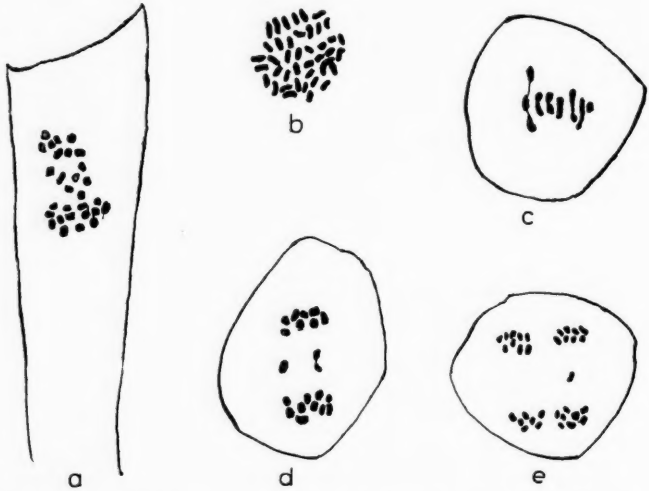


Fig. 3. *S. viminalis* × *gigantea*. — *a*: A 1 eines triploiden ♀-Strauches. — *b*—*e*: Ein aneuploider ♂-Strauch. — *b*: Somatische Kernplatte. — *c*: M 1. — *d*: A 1. — *e*: A 2.

sehr häufig, aber die überwiegende Mehrzahl der Pollenkörner muss eine intermediäre Chromosomenzahl gehabt haben (zwischen 19 und 38), und die Rückkreuzung sollte theoretisch hauptsächlich aus aneuploiden Sträuchern bestanden haben. Wann die Selektion erfolgt ist, kann unmöglich entschieden werden. Zuerst hat man mit einer Gametenselektion zu rechnen, ferner kann eine Zygotenelimination stattgefunden haben, die zu nicht keimfähigen Samen führt, und schliesslich hat sicherlich eine Selektion unter den jungen Pflanzen stattgefunden, bevor diese ins Blütenstadium gelangt sind, indem die aneuploiden Individuen abgestorben sind. Es ist ja früher bekannt, dass Aneuploide häufig schwächere Vitalität zeigen; vor kurzem nachgewiesen für die

Kreuzung triploides *Dactylis* (*Aschersoniana* × *glomerata*) × *Aschersoniana*. Die Pflanzen mit intermediären Zahlen waren hier am schwächsten, die mit Zahlen, die sich den Eltern nähern, waren kräftiger, und die einzige ganz vitale Pflanze war rein diploid (= *Aschersoniana*). (MÜNTZING, 1937, S. 162.)

In dieser *Dactylis*-Kreuzung wurden, trotzdem nur 16 Pflanzen untersucht werden konnten, die Chromosomenzahlen 14—20 gefunden. Die Mutterpflanze war hier ein triploider Bastard. Aber in mehreren Fällen hat sich herausgestellt, dass gewisse Chromosomenzahlen, gern solche die etwas höher als die diploide sind, in den Nachkommen dominieren. Bei Verwendung der triploiden Form als Vaterpflanze pflegt die Selektion noch ausgeprägter zu sein. So schon in den bekannten *Oenothera*-Kreuzungen, in denen triploides ♀ × diploides ♂ stark variierende Chromosomenzahlen gibt, diploides ♀ × triploides ♂ nur diploide und triploide Zahlen (VAN OVEREEM, 1921). Hier handelt es sich offenbar, wie VAN OVEREEM hervorhebt, um Gametenselektion, sonst wären gewisse Zygoten in der ersten Kreuzungsrichtung, aber nicht in der anderen lebensfähig. Als ein weiteres Beispiel für reziprok verschiedene Resultate seien erwähnt Kreuzungen zwischen diploiden und triploiden *Petunia*-Formen, triploide ♀ × diploide ♂ gaben die Chromosomenzahlen 14—20, die reziproke Kreuzung nur diploide Pflanzen (LEVAN, 1937). Da im hier vorliegenden *Salix*-Fall die Kreuzung triploides ♀ × diploides ♂ nicht untersucht ist, besteht noch geringere Möglichkeit sich darüber zu äussern, wann hier die Selektion stattgefunden hat.

EINIGE DIPLOIDE BASTARDE.

Salix purpurea × *hastata*. — Es wurden die Teilungen in einem männlichen Strauch studiert. Dieser Bastard entstand durch Kreuzung von diploiden Arten; er war auch diploid. Eine vollständige Paarung zwischen den Chromosomen der beiden Arten war die Regel, nur in einer geringen Anzahl von Pollenmutterzellen gab es univalente Chromosomen. Die Fixierungen sind nicht gut ausgefallen. In quergeschnittenen Metaphase 1-Platten wurden einigemale 19 Einheiten gesehen (Fig. 4 *a*), aber in recht vielen wurde ungefähr diese Zahl gefunden und wahrscheinlich gibt es fast immer 19 Bivalente. Diese lagen in der Platte gern in etwas verschiedener Höhe, was bei *Salix* recht häufig ist. Die Anaphase 1 verlief regelmässig (Fig. 4 *b*) und nur in Ausnahmefällen wurden zurückgebliebene Chromosomen gefunden.

Die zweite Teilung war auch regelmässig (Fig. 4 *c*), wenngleich auch nun mitunter Chromosomen zwischen den Telophasengruppen zurückgeblieben waren. In einem Pollenfach mit Tetraden wurde eine Diade beobachtet (Fig. 4 *d*). Die Kerne waren bedeutend grösser als in den Tetradenzellen. Es sind offenbar diploide Pollenzellen gebildet worden, und es ist von Interesse festzustellen, dass die Kerne der Diaden-

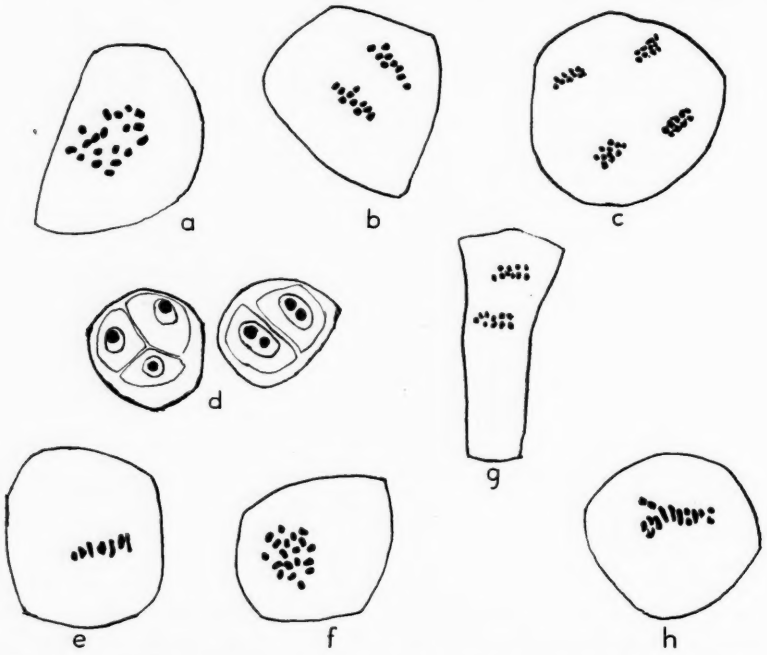


Fig. 4. — *a—d*: *S. purpurea* × *hastata*. — *a*: M 1. — *b*: A 1. — *c*: A 2. — *d*: Pollen-»Tetraden». — *e—f*: *S. aurita* × *hastata*. — *e*: M 1. — *f*: M 1 quergeschnitten. — *g*: *S. viminalis* × *aurita*, A 1. — *h*: *S. viminalis* × *daphnoides*, M 1.

zellen infolge der verdoppelten Chromosomenzahl zwei Nukleolen anstatt eines enthalten.

Der Pollen dieses Bastards war gut. Leere Körner gab es allerdings, aber ihre Anzahl war gering, weniger als 10 %.

Salix aurita × *hastata*. — Die Meiosis war bei diesem Bastard regelmässig. In gut fixierten Pollenmutterzellen konnte man in der Metaphase 1 19 Bivalente sehen. Fig. 4 *e* zeigt die Metaphase 1 in Seitenansicht, Fig. 4 *f* in Polansicht. Univalente Chromosomen wur-

den nur selten beobachtet, das Vorkommen von Multivalenten konnte nicht mit Sicherheit nachgewiesen werden. Die *aurita*- und *hastata*-Chromosomen paaren sich also vollkommen normal miteinander. Zuweilen wurde eine verspätete Trennung von Chromosomen in einem Bivalent beobachtet. Ein interstitielles Chiasma ist gebildet worden, was gern eine Erschwerung der Separation mit sich bringt. Wo die Chiasmata im allgemeinen terminal sind, verursacht das zufällige Vorkommen von interstitiellen Chiasmata daher das Bild von verspäteten Chromosomen während der Anaphase. Die zweite Teilung war auch sehr normal und der Pollen hat ungefähr das Aussehen wie bei *purpurea* × *hastata*.

Salix repens × *viminalis*. — Auch bei diesem Bastard war die Chromosomenpaarung normal; in den Pollenmutterzellen werden Bivalente gebildet. Die Anzahl war schwer zu bestimmen, da die Teilungen etwas undeutlich waren, aber man sah in günstigen Fällen gegen 19 Chromosomenassoziationen. Die zweite Teilung war normal.

Salix viminalis × *aurita*. — Die Reduktionsteilung dieses Strauches musste in Embryosackmutterzellen studiert werden, da nur Fixierungen von weiblichen Sträuchern vorlagen. Sie erfolgt sehr früh, noch bevor das Integument gleiche Höhe mit dem Nuzellusscheitel erreicht hat. Die *viminalis*-Chromosomen paaren sich gut mit den *aurita*-Chromosomen und bilden Bivalente. Die erste Anaphase verlief ohne Störungen (Fig. 4 *g*).

Salix viminalis × *daphnoides*. — Dieser Bastard hatte gleichfalls eine gute Chromosomenpaarung mit Bivalenten und in quergeschnittenen Kernplatten wurden 19 solche gezählt. Nicht selten kam indessen Nonkonjugation vor, was sich im Auftreten von Univalenten zu erkennen gab (Fig. 4 *h*). In Pollenfächern mit der ersten Teilung sah man hier und da Pollenmutterzellen, in denen der Kern in der Prophase verblieben war.

Letztgenanntes war in den Antheren eines intersexuellen Strauches noch häufiger. Hier befanden sich etwa $^1/_3$ der Zellen in einem Prophasestadium, in dem der Kern gross und fast leer war, nur ein grosser Nukleolus war zu sehen, der sich häufig einmal teilte. Im gleichen Fach gab es ferner verschiedene Stadien von der Metaphase 1 bis zu fertigen Tetraden, während es sonst Regel ist, dass die Pollenmutterzellen des gleichen Faches sich in etwa gleichem Teilungsstadium befinden. Für eingehendere Studien waren die Teilungen zu schlecht fixiert, sie hatten einen regelmässigen Verlauf. Der Strauch war ungefähr diploid und konnte höchstens 1—2 Chromosomen mehr oder

weniger als die normale Zahl haben. Die Intersexualität ist demnach von keiner grösseren Veränderung der Chromosomenzahl begleitet.

Zusammenfassend kann man also sagen, dass die hier untersuchten Bastarde alle gute Chromosomenpaarung zeigten. In allen studierten Kombinationen zeigten die Chromosomen starke Affinität.

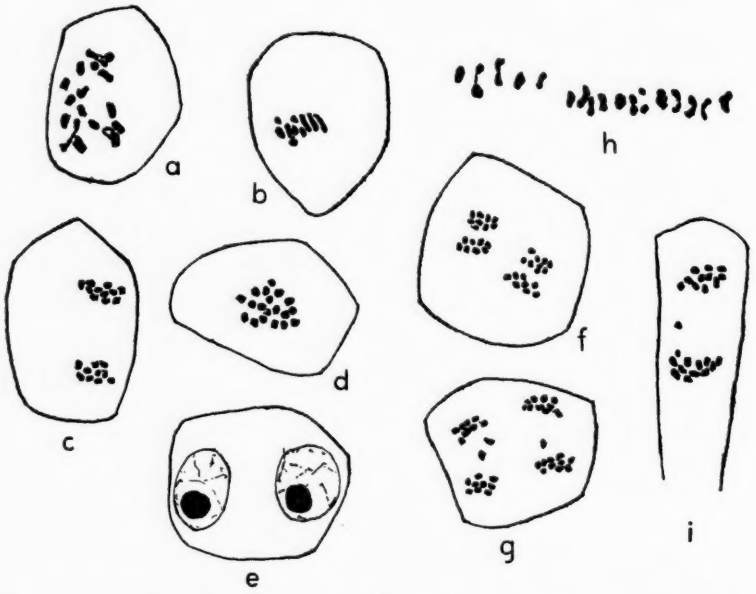


Fig. 5. *S.* (*purpurea* × *daphnoides*) × (*repens* × *aurita*). — *a*—*g*: ♂-Strauch. — *a*: Metakinese. — *b*: M 1. — *c*: A 1. — *d*: M 1 quergeschnitten. — *e*: Interkinese. — *f* und *g*: A 2. — *h*—*i*: ♀-Strauch. — *h*: Die Chromosomen in M 1, $2_{III} + 15_{II}$. — *i*: A 1.

SALIX (PURPUREA × DAPHNOIDES) × (REPENS × AURITA).

Dieser quaternäre Bastard ist von HERIBERT NILSSON (1937, S. 362) kurz erwähnt worden. Er ist aus vier diploiden Arten gebildet. Seine Darstellung aus den beiden binären Bastarden war leicht, es wurden 642 Individuen aufgezogen. Ich habe die Meiosis eines männlichen und eines weiblichen Strauches untersucht. Beide waren diploid; aber es ist natürlich möglich, dass es unter den nicht untersuchten Sträucher mit abweichender Chromosomenzahl gibt.

Die Meiosis verläuft ungefähr wie bei den früher behandelten diploiden Bastarden, jedoch sind Störungen allgemeiner vorkommend. Die Chromosomenpaarung ist meistens vollständig, es werden 19 Bivalente gebildet. Fig. 5 *a* zeigt das Metakinese-Stadium, in dem diese Chromosomenpaarung stattfindet, Fig. 5 *d* eine quergeschnittene Metaphase 1 mit 19 Einheiten. Nicht selten gab es jedoch univalente Chromosomen (Fig. 5 *b*), die eine Nonkonjugation zwischen den Chromosomen anzeigten. Die Anaphase 1 war regelmässig (Fig. 5 *c*), nur seltener wurde ein zurückgebliebenes Chromosom beobachtet. Dieses wurde jedoch nicht eliminiert sondern einem Tochterkern einverleibt; während der Interkinese gab es keine Spur von Elimination (Fig. 5 *e*). Die zweite Teilung war meistens regelmässig (Fig. 5 *f*), aber zuweilen blieben die Chromosomen während der Anaphase zurück (Fig. 5 *g*). In der Regel wurden diese zurückgebliebenen Chromosomen einer der Tochterplatten einverleibt; die allermeisten Pollentetraden hatten vier Zellen, aber selten sah man »Tetraden» mit einer kleinen überzähligen fünften Zelle zufolge von Störungen während der zweiten Teilung. Der Pollen des zytologisch untersuchten Strauches zeigte einen recht hohen Grad von Sterilität, indem ca. 15 % der Körner leer waren. Es ist dies ein höherer Prozent als man auf Grund des Aussehens der Tetraden und des Verlaufes der Reduktionsteilung erwarten könnte, deutet aber darauf hin, dass haplontisch letale Chromosomenkombinationen gebildet werden.

Auch der weibliche Strauch zeigte eine gute Chromosomenpaarung. Univalente Chromosomen wurden nicht beobachtet, es wurde jedoch kein grösseres Material untersucht. Trivalente schienen mitunter gebildet zu werden. Fig. 5 *h* zeigt die Chromosomen in einer Metaphase 1. Es gibt zwei Trivalente. Sie sehen allerdings aus wie heteromorphe Chromosomenpaare, aber das ist nur scheinbar, dadurch verursacht dass zwei Chromosomen intim vereinigt sind. Im Bivalent ganz rechts gibt es ein interstitielles Chiasma, was auch bei reinen Arten von *Salix* ungewöhnlich ist. Die Anaphase 1 war regelmässig. Im allgemeinen wurden keine zurückgebliebenen Chromosomen beobachtet, aber während der frühen Anaphase konnten welche vorkommen (Fig. 5 *i*).

SALIX VIMINALIS × PHYLICIFOLIA.

Dieser Bastard ist durch Kreuzung einer diploiden mit einer hexaploiden Art entstanden. Er ist also tetraploid. Es zeigte sich, dass die Meiosis ganz regelmässig wie bei einer reinen Art war.

In der Metaphase 1 gab es oft nur Bivalente. Fig. 6 *c* zeigt eine quergeschnittene Metaphase mit 38 Bivalenten, Fig. 6 *a* zeigt eine beginnende Anaphase 1. Zuweilen gab es jedoch ein Quadrivalent. In der in Fig. 6 *b* abgebildeten quergeschnittenen Platte war ein solches sichtbar, so auch in Fig. 6 *d*. Gelegentlich kommen einzelne Univalente vor. Wie aus den quergeschnittenen Platten hervorgeht, liegen die Bivalente gern in Gruppen beieinander, häufig drei zusammen. Diese Erscheinung kann ja als eine sog. sekundäre Assoziation gedeutet werden, aber es erscheint sehr zweifelhaft, ob eine solche Deutung dieser Gruppenbildung richtig ist. Recht häufig liegen zwei Bivalente nebeneinander.

Die Anaphase 1 war sehr regelmässig; die Chromosomen gingen in zwei gleichen Gruppen auseinander (Fig. 6 *h*), und nur seltener waren zurückgebliebene Chromosomen, wahrscheinlich als Folge von Multivalentbildung (Fig. 6 *g*), zu beobachten. Die Chromosomenverteilung war meistens 38 + 38 (Fig. 6 *e*); in einem Schnitt durch ein Pollenfach mit günstig fixierten Pollenmutterzellen wurde diese Verteilung in sieben Zellen gefunden, während es in einer Zelle 40 Chromosomen in einer Anaphasenplatte, 37 in der anderen gab. Man kann vermuten, dass im letztgenannten Fall eines der Chromosomen eine zu frühe Teilung erfahren hat (Fig. 6 *f*). Die zweite Teilung war auch sehr regelmässig.

In der Metaphase 2 ist die Chromosomenzahl sehr schwer zu bestimmen, da die Chromosomen sehr nahe nebeneinander liegen und mitunter zu verschmelzen scheinen. Es muss indessen als sehr ungewiss betrachtet werden, dass dies auf eine sekundäre Affinität zwischen den Chromosomen zurückzuführen ist. Es gab Zellen, in denen die Chromosomen sehr gut getrennt lagen (Fig. 6 *j*), obgleich zuzugeben ist, dass auch in einigen anscheinend sehr gut fixierten Zellen die Chromosomen paarweise (Fig. 6 *i*), jedoch nicht in Gruppen von drei wie während der ersten Teilung, lagen. Die Assoziation in dieser Teilung beweist demnach keine Art von Affinität zwischen den Chromosomen innerhalb des 19-chromosomigen Genoms, aber vielleicht eine Affinität zwischen homologen Chromosomen verschiedener Genome. Die Pollentetraden haben normales Aussehen und die Pollenkörner sind gleichgross und gut entwickelt.

Die Meiosis dieses Bastardes zeigt, dass die Chromosomen in einem der drei *phylicifolia*-Genome sich mit den *viminalis*-Chromosomen paaren. Die beiden anderen Genome sind offenbar miteinander übereinstimmend, da ihre Chromosomen sich paaren. Wahrscheinlich sind

indessen alle drei Genome gleich, und *S. phylicifolia* ist eine Autopolyploide, nämlich eine Autohexapolyploide mit drei strukturell gleichen Genomen, die ihrerseits mit dem *viminalis*-Genom übereinstimmen. Dies braucht jedoch nicht so gedeutet zu werden, dass die Art notwendigerweise eine intraspezifische Polyploide ist. Die drei Genome können sehr wohl von verschiedenen diploiden Arten herstammen; die Chromosomenpaarung der diploiden Bastarde zeigt wie nahe verwandt in struktureller Hinsicht die verschiedenen Artgenome sind. Man würde

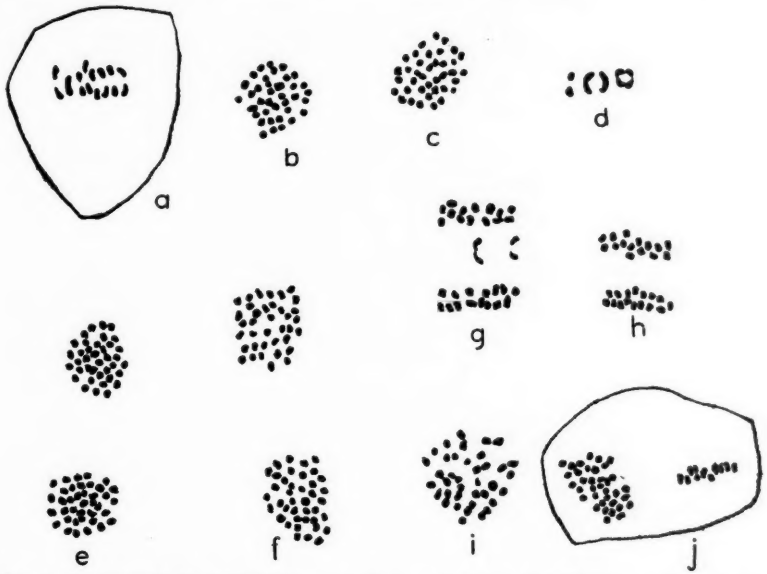


Fig. 6. *S. viminalis* × *phylicifolia*. — *a*: M. 1. — *b* und *c*: M 1-Platten. — *d*: $3_{II} + 1_{IV}$. — *e* und *f*: Zwei A 1. — *g* und *h*: A 1. — *i*: M 2. — *j*: M 2.

vielleicht eine ausgesprochenere Multivalentbildung bei *S. phylicifolia* und *viminalis* × *phylicifolia* erwartet haben, aber bei diesen beiden Typen gibt es fast nur Bivalente. Multivalente mit mehr als drei Chromosomen werden jedoch bei *Salix* nicht so leicht gebildet. Die experimentell dargestellte *neocinerea* zeigte nur einzelne Quadrivalente und dies nicht in allen Embryosackmutterzellen.

Es gibt mancherlei Beispiele dafür, dass der tetraploide Bastard zwischen einer diploiden und einer hexaploiden Art infolge von Autosyndese eine ganz normale Meiosis mit Bivalenten hat. Einige Fälle aus der neueren Literatur seien erwähnt. *Fragaria nipponica* ist di-

ploid (2n = 14), *F. elatior* autopolyploid (2n = 42). Der Bastard hat normale Teilungen, aber in der Metaphase 1 nur Bivalente, ausnahmsweise ein Quadrivalent. Seine Meiosis verhielt sich wie bei einer tetraploiden Art, weshalb er den Namen *F. elnipponica* erhielt (LILIENFELD, 1936). In ähnlicher Weise verhalten sich *Phleum pratense* (2n = 42) × *Ph. nodosum* (2n = 14) (NORDENSKIÖLD, 1937), ferner mehrere *Chrysanthemum*-Bastarde (SHIMOTOMAI, 1933). Die Grundzahl in der letztgenannten Gattung ist bekanntlich 9. Bastarde, entstanden durch Kreuzung von Arten, von denen die eine somatisch 18 Chromosomen mehr hatte als die andere, verhielten sich zytologisch wie neue Arten. Die Meiosis zeigte nämlich nur Bivalente und ihre Nachkommen hatten eine konstante Chromosomenzahl.

S. viminalis × *phylicifolia* hat eine ähnliche Zytologie wie die als neue Arten aufgefassten *Fragaria*- und *Chrysanthemum*-Bastarde. Er ist auch sehr fertil; Kreuzungen zwischen männlichen und weiblichen Sträuchern gaben einen reichlichen Samenansatz (HERIBERT NILSSON, 1930, S. 37). Eine genische Variation unter den Nachkommen muss die Folge davon sein, dass 19 Bivalente von Chromosomen verschiedener Arten gebildet worden sind. Die Chromosomenzahl verbleibt jedoch konstant, die Gameten haben nämlich fast alle 38 Chromosomen.

Einige kompliziertere Artbastarde, die *viminalis* × *phylicifolia* als einen der Eltern enthalten, sind von HERIBERT NILSSON 1930 beschrieben worden. Solche Bastarde habe ich nur in unbedeutendem Grade untersucht. *S.* (*cinerea* × *phylicifolia*) × (*viminalis* × *phylicifolia*) zeigte in der Metaphase 1 recht viele univalente Chromosomen. Dies beruht indessen darauf, dass *cinerea* × *phylicifolia* eine ziemlich unregelmässige Meiosis hat, wodurch seine Gameten zur Entstehung von aneuploiden Bastarden führen. *S.* (*repens* × *phylicifolia*) × (*viminalis* × *phylicifolia*) habe ich nicht untersucht. Sie dürfte tetraploid sein und normale Chromosomenpaarung haben. Laut HERIBERT NILSSON ist es ein recht einheitlicher Bastard mit hauptsächlich *phylicifolia*-Charakteren, aber überdies treten Eigenschaften von *repens* und *viminalis* zutage. Nach der vermuteten Chromosomenzusammensetzung sollte er fertil sein. Laut HERIBERT NILSSON waren die Kapseln leer, aber eine richtige Untersuchung der Fertilität konnte nicht stattfinden, da die Kreuzung nur zu weiblichen Sträuchern geführt hat (l. c.). Einen reichlicheren Samenansatz sollte man höchstens bei Kreuzung mit einem tetraploiden Typus erwarten. Ein anderer hierhergehöriger Bastard ist die sog. *S. septemgena* (l. c.). Er ist dargestellt worden durch Pollination des sechsfachen Bastards (spont. *cinerea* × *purpurea*)

× *aurita* × (*viminalis* × *caprea*) × *daphnoides* mit Pollen von *viminalis* × *phylicifolia*. Die Kreuzung führte zu einer recht grossen Anzahl von Sträuchern (49 Stück). Es ist wohl am wahrscheinlichsten, dass dieser Bastard triploid ist. Damit stimmt auch überein, dass er sehr steril ist. Die Kreuzung zwischen männlichen und weiblichen Sträuchern, die hier ausgeführt werden konnte, gab kein Resultat (l. c. S. 38).

In Kreuzungen prävaliert *S. phylicifolia* in recht hohem Grad. Die Anzahl *phylicifolia*-Chromosomen überwiegt bei Kreuzung mit diploiden Arten, ob nun reine *phylicifolia* oder der Bastard teilnimmt. Diese Prävalenz bestätigt die Autopolyploidie.

SALIX CINEREA-BASTARDE.

Es sind Bastarde zwischen *S. cinerea* und verschiedenen anderen Arten untersucht worden und eine Beschreibung der Meiosis derselben soll hier mitgeteilt werden. Vorerst sei jedoch eine für die verschiedenen Bastarde gemeinsame Eigentümlichkeit in der Entwicklung der Samenanlagen erwähnt. Meiosis ist stark verzögert. Bei den meisten *Salix*-Arten erfolgt die Meiosis recht früh, ungefähr wenn das Integument gleiche Höhe mit dem Scheitel des Nuzellus erreicht hat, aber bei den *cinerea*-Bastarden erst wenn der Mikropylarkanal seit langem fertiggebildet und die Samenanlage fertig ist. Es ist schwer zu wissen, worauf diese Verspätung zurückzuführen ist. Bei weiblichen Sträuchern von *S. cinerea* kommt sie nicht vor, die Entwicklung erfolgt normal; diese Eigentümlichkeit ist also nicht von dieser Art ererbt worden. Ferner findet die Verspätung nur in den Embryosackmutterzellen statt, bei männlichen Sträuchern scheint sie nicht aufzutreten. Männliche *cinerea*-Bastarde sind allerdings nicht leicht zu erhalten, weil in den Kreuzungen meistens weibliche entstehen. Ein paar wurden jedoch untersucht. Bei diesen gab es kaum eine Verspätung. In sehr jungen Ähren von *repens* × *cinerea* war die Meiosis abgeschlossen. In männlichen Sträuchern von Kreuzungen zwischen *cinerea* und *viminalis* × *caprea*-Derivaten konnte keine grössere Verspätung mit Sicherheit festgestellt werden. Es scheint sich also nicht so zu verhalten, dass das späte Eintreffen von Diakinese und Metaphase 1 darauf beruht, dass die *cinerea*-Chromosomen sich nur sehr langsam mit Chromosomen anderer Arten paaren. Die Anzahl von Chromosomen, also der Umstand, dass die *cinerea*-Bastarde tri- oder pentaploid sind, wirkt kaum ein. Bei triploiden *viminalis* × *caprea* fand die Metaphase 1 in normaler Zeit statt.

Diese Verspätung der Teilungen habe ich nicht nur bei allen untersuchten *cinerea*-Bastarden sondern auch bei einigen anderen Formen angetroffen. So war sie sehr ausgeprägt bei *S. laurina*, die aus der Kreuzung *viminalis* × *caprea* hervorgegangen ist (HÅKANSSON, 1929), und ferner in weiblichen Sträuchern von *S.* (*viminalis* × *daphnoides*) × (*viminalis* × *phylicifolia*). Die Verspätung im letztgenannten Fall war nicht gleich stark, aber die Teilungen trafen doch erst ein, nachdem der Mikropylarkanal gebildet war.

Sämtliche diese Bastarde [auch *S.* (*viminalis* × *daphnoides*) × (*viminalis* × *phylicifolia*)] mit verzögerter Entwicklung des Embryosackes haben das gemeinsam, dass sie fast vollkommen steril waren. Nur ausserordentlich selten werden in den Kapseln keimfähige Samen gebildet.

S. caprea × *cinerea*. — Dieser triploide Bastard zeigt sehr starke Sterilität. Es ist nicht gelungen bei Kreuzung mit den Elternarten entwicklungsfähige Samen zu erhalten (HERIBERT NILSSON, 1931).

Die Entwicklung war sehr stark verspätet. Die ältesten untersuchten Fruchtknoten hatten voll entwickelte Narben und zahlreiche Bienen krochen auf denselben umher. Die Samenanlagen waren fertig, aber die meisten enthielten eine ungeteilte Embryosackmutterzelle mit ungeteiltem Kern oder mit einem in Teilung begriffenen Kern. In den Samenanlagen, in denen die Entwicklung am weitesten gekommen war, gab es einen zweikernigen Embryosack. In dieser Samenanlage könnte vielleicht ein befruchtungsfähiger Embryosack gebildet worden sein, und unter der Voraussetzung, dass die Pollenschläuche das Vermögen haben im Fruchtknoten eine Zeitlang zu leben, auch ein Embryo. Die Makrosporen degenerierten meistens.

In älteren Fruchtknoten enthielten stets mehrere Samenanlagen Metaphase 1, was darauf deutet, dass dieses Stadium verhältnismässig lange dauert. In bezug auf die Chromosomenpaarung ist hervorzuheben, dass die Anzahl Univalente gross ist; sie variiert jedoch recht stark. Die Anzahl von Trivalenten ist entsprechend gering. Studiert man quergeschnittene Platten, kann man solche mit bis zu 37 Einheiten finden (Fig. 7 *e*), in solchen gibt es also nur ein Trivalent auf 18 Univalente. In anderen Platten gab es eine kleinere Anzahl, etwas mehr als 30 Einheiten wurden in mehreren Fällen gezählt. Es ist jedoch ganz offenbar, dass die meisten Chromosomen vom einen *cinerea*-Genom ungepaart verbleiben. Zur gleichen Auffassung gelangt man bei einem Studium der Metaphase 1, betrachtet von der Seite.

Häufig konnte man nicht ein einziges sicheres Trivalent feststellen, aber zahlreiche Univalente lagen auf beiden Seiten der Äquatorialebene, wo die Bivalente sich in etwas verschiedener Höhe befanden (Fig. 7 *c* und *d*). Gewöhnlich waren jedoch einige Trivalente vorhanden (Fig. 7 *a* zeigt vier). In einigen Embryosackmutterzellen war die Anzahl von Univalenten sehr gross, mehr als 19 (siehe Fig. 7 *b*). Hier gab es eine

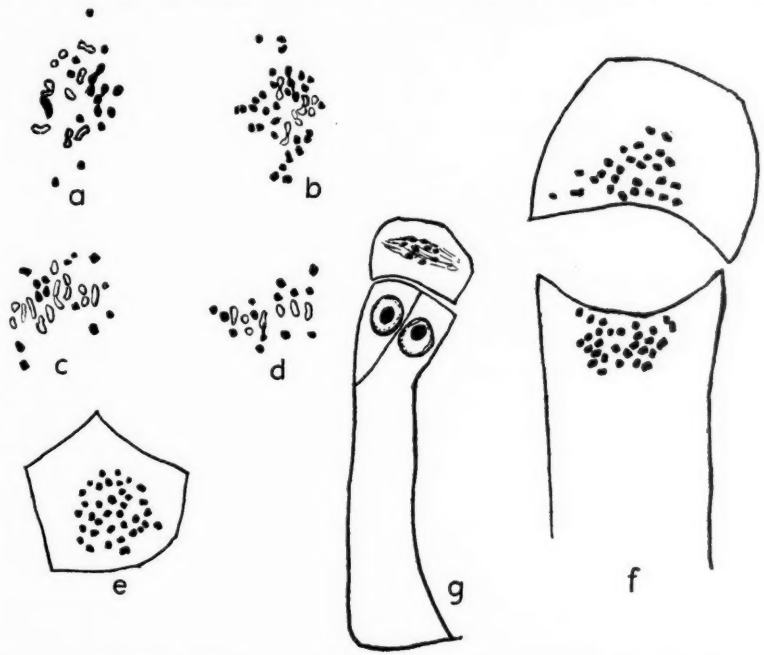


Fig. 7. *S. caprea* × *cinerea*. — *a*: Metakinese. — *b*: M 1, die A 1 fängt allmählich und langsam an. — *c* und *d*: M 1. Die Bivalente sind nur im Umriss, Uni- und Trivalente schwarz gezeichnet. — *e*: M 1 quergeschnitten. — *f*: M 2. — *g*: Makrosporen, verspätete Teilung in der mikropylaren Diadenzelle.

frühe Anaphase, in der die Chromosomen langsam sich trennten und verschieden früh in den verschiedenen Bivalenten. Die zweite Teilung wurde dadurch gekennzeichnet, dass die Kernspindeln in beiden Diadenzellen oft quergestellt waren; ein Längsschnitt durch den Nuzellus konnte beide Platten treffen (Fig. 7 *f*, in jeder sieht man 27—28 Chromosomen). Die Makrosporen liegen häufig, aber nicht immer, in gleicher Höhe (Fig. 7 *g*).

S. viminalis × *cinerea*. — Dieser Bastard ist auch sehr steril, er

bildet niemals Samen aus. Hier wurde eine ähnliche Erscheinung wie bei *caprea* × *cinerea* gefunden. Die Entwicklung in den Samenanlagen ist jedoch in verschiedenen Jahren verschieden weit gekommen. In dem 1933 eingesammelten Material wurde niemals eine Teilung des Kerns der Embryosackmutterzelle beobachtet. Die Zelle degenerierte, ohne dass der Kern überhaupt das Diakinesestadium erreichte. Im 1937 eingesammelten Material ging die Entwicklung weiter, obgleich es von einem Strauch eingesammelt wurde, der eine vegetative Vermehrung des vorigen war. In voll entwickelten Fruchtknoten enthielten die Samenanlagen häufig Makrosporen, die Teilungen hatten stattgefunden, obgleich stark verspätet. Ein reifer Embryosack wurde jedoch nicht beobachtet. In den Samenanlagen in Fruchtknoten, die so alt waren dass ihre Narben verwelkt waren, hatten sich keine Embryosäcke entwickelt.

S. purpurea × *cinerea.* — Bei diesem Bastard war die Degeneration sehr stark. Die Embryosackmutterzelle degenerierte ohne dass sich ihr Kern teilte. Nur in einer einzigen Samenanlage wurde eine sehr stark verspätete Metaphase 1 beobachtet. Die Embryosackmutterzelle wird wie bei anderen *cinerea*-Bastarden sehr lang. In alternden Zellen wandert ihr Kern gern von seinem ursprünglichen Platz im mikropylaren Teil hinunter in das chalazale Ende der Embryosackmutterzelle.

S. repens × *cinerea.* — Von diesem Bastard konnte nur wenig Material untersucht werden. Eine Meiosis trat hier ein, aber ein Embryosack wurde kaum entwickelt. Beobachtungen über die Chromosomenpaarung konnten nicht gemacht werden.

S. aurita × *cinerea.* — Die Entwicklung war wie gewöhnlich sehr verspätet. Es wurde kein fertiger Embryosack gesehen und wird wohl selten gebildet. Dagegen findet oft eine Meiosis statt. Die Metaphase 1 war nicht so deutlich, die Fixierung war nämlich nicht gut gelungen. Die Anzahl Univalente war nicht gering, erschien aber geringer als bei *caprea* × *cinerea.* Viele der überzähligen *cinerea*-Chromosomen hatten sich gepaart und wahrscheinlich haben sie Trivalente mit einem *aurita*- und einem *cinerea*-Chromosom gebildet. Es war jedoch aus dem angegebenen Grunde unmöglich zwischen Bi- und Trivalenten sicher zu unterscheiden. Während der Anaphase 1 kam es zu Unregelmässigkeiten, die eine Elimination von Chromosomen bedingen konnten. Die zweite Teilung führte allerdings mitunter zur Bildung von vier Makrosporen, aber häufig blieb die Wandbildung aus und die Embryosackentwicklung begann nach dem *Scilla*-Schema.

S. cinerea × *phylicifolia.* — Dieser Bastard ist entstanden durch Kreuzung einer tetraploiden und einer hexaploiden Art. Er war auch pentaploid. Es konnte ein grosses Material untersucht werden.

Die Meiosis in der Embryosackmutterzelle ist auch hier verspätet, aber es wird recht oft ein fertiger Embryosack im Nuzellus gebildet. Häufig degenerierten die Embryosackmutterzellen vor der Teilung. Die Makrosporen lagen oft zu zwei in gleicher Höhe. Sehr häufig degenerierten sie. In anderen Fällen erfolgte eine Entwicklung und nicht selten haben sich aus ein paar Makrosporen im gleichen Nuzellus Embryosäcke gebildet. Der Embryosack war achtkernig und reichte zuweilen in den Mikropylarkanal hinaus, aber häufig war die Nuzellusepidermis intakt. Es war oft recht anormal. Es wurde z. B. beobachtet, dass alle drei Zellen im Eiapparat den Kern im mikropylaren Teil hatten. Überzählige Zellen oder Kerne konnten vorkommen. So wurde ein Embryosack mit drei Antipoden, zwei Polkernen in Kontakt, aber im Mikropylenende mit sieben Zellen oder Kernen gesehen. In einem anderen Embryosack gab es am Antipodenende zehn Zellen, im Mikropylenende drei grosse und vier kleine Zellen, in der Mitte des Embryosackes zwei recht kleine freie Kerne. HERIBERT NILSSON hat für diesen Bastard eine schwache Fertilität konstatiert, trotzdem es keine männlichen Sträucher desselben als Pollenlieferanten gab.

Eine vollständige Analyse der Metaphase 1 konnte wegen der ziemlich grossen Anzahl Chromosomen und des verhältnismässig engen Platzes nicht durchgeführt werden. In quergeschnittenen Platten lagen die Chromosomen allzu dicht um gezählt werden zu können. Die Kernspindel liegt der mikropylaren Oberfläche der langen Embryosackmutterzelle sehr nahe. Die Anzahl von Univalenten ist gross und sie liegen nahe der Äquatorialebene, weshalb sie schwierig zu zählen sind. Fig. 8 *a* zeigt zwei Schnitte einer Metaphase 1. Es konnten nur $^2/_3$ der Gesamtanzahl von Chromosomen abgebildet werden. Es ergibt sich, dass es viele Univalente gibt, während die konjugierten Chromosomen meistens Bivalente bilden. Ausserdem gibt es vier Trivalente und wahrscheinlich ein Quadrivalent. Die Anzahl von Multivalenten und Univalenten wechselt in verschiedenen Zellen. Die Anaphase 1 verlief stets mit Störungen (Fig. 8 *b*), zwischen den Tochterplatten konnten zurückgebliebene Multi-, Bi- und Univalente beobachtet werden. Eine Bestimmung der Chromosomenzahl in den Anaphasenplatten konnte nicht erfolgen. Nach der Bildung von Kernmembranen zeigte es sich, dass nicht selten Chromosomen eliminiert wurden.

S. (*viminalis* × *caprea*) × *cinerea.* — Diese Kombination wurde

durch Pollination von Strauch 13 in F_1 der alten *S. viminalis* × *caprea*-Kreuzung mit *cinerea* erhalten. Sowohl männliche wie weibliche Sträucher wurden untersucht. Sie waren wie erwartet triploid.

Die Chromosomenpaarung in der Metakinese (Fig. 8 *f*) und Metaphase 1 (Fig. 8 *c* und *d*) zeigt Tri-, Bi- und Univalente. Die Anzahl Univalente variiert, ist aber ziemlich gross. Quergeschnittene Meta-

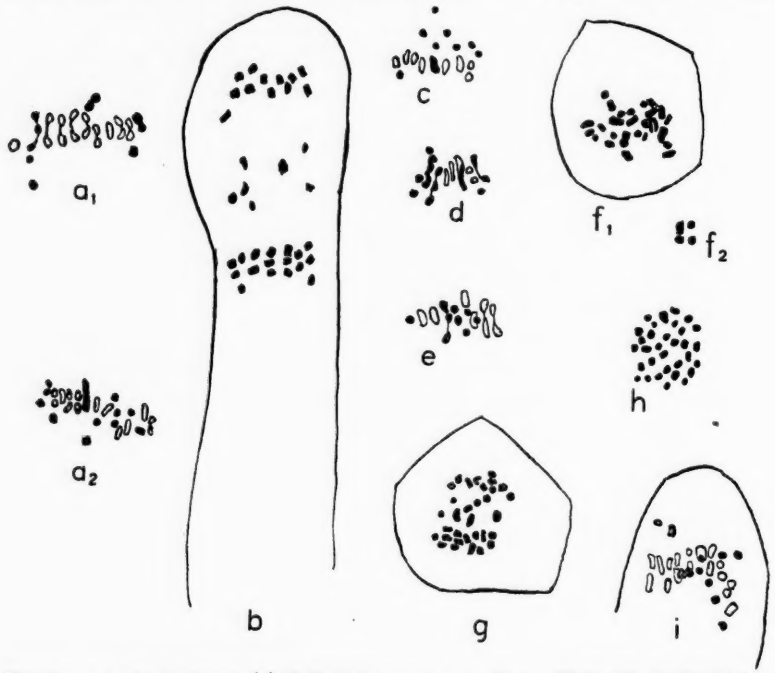


Fig. 8. — *a*—*b*: *S. cinerea* × *phylicifolia*. — a_1—a_2: M 1. Nicht alle beobachteten Chromosomen sind eingezeichnet. — *b*: A 1. — *c*—*i*: *S.* (*viminalis* × *caprea*) × *cinerea*. — *c*—*e*: M 1. — f_1—f_2: Metakinese. — g: A 1. — *h*—*i*: ♀-Strauch. — *h*: M 1 quergeschnitten. — *i*: M 1.

phasen 1 zeigen meistens 28—32 Einheiten, also 9—13 Univalente. Ein sicheres Unterscheiden von Tri- und Bivalenten ist nicht immer möglich. Man sollte 6—10 Trivalente erwarten und diese Anzahl schien auch vorzukommen. Eine Autosyndese zwischen den *cinerea*-Chromosomen ist demnach nicht wahrscheinlich. Die Anaphase 1 war äusserst unregelmässig mit zahlreichen zurückgebliebenen Chromosomen (Fig. 8 *g*), die indessen allmählich ihre Pole erreichten und in die Tochterkerne eingeschlossen wurden. Während der Interkinese gab es

im allgemeinen keine Mikrozyten oder andere Spuren einer Chromosomenelimination. Während der zweiten Teilung waren die Chromosomen in der Metaphase stark zusammengeballt. Die Anaphase 2 zeigte gern Störungen. Diese hatten zur Folge, dass die Pollentetraden oft eine oder mehrere überzählige kleine Pollenzellen enthielten.

Bei den weiblichen Sträuchern erfolgte, wie erwartet, die Reduktionsteilung sehr spät. Die Metaphase 1 verlief wie bei den männlichen Sträuchern (Fig. 8 *h* und *i*). Die Anaphase 1 zeigte Störungen, die zur Elimination von Chromosomen führten.

Die Chromosomenpaarungen der triploiden *cinerea*-Bastarde zeigen, dass wenigstens etwa 19 Bivalente und Trivalente gebildet werden. Aber die Anzahl Univalente ist stets verhältnismässig gross, was besonders deutlich zutage tritt, wenn man die Paarung bei (*viminalis* × *caprea*) × *cinerea* mit der bei triploider (*viminalis* × *caprea*) vergleicht. In beiden Fällen konnten männliche Sträucher untersucht werden, aber die Trivalentbildung war im letztgenannten Bastard entschieden ausgeprägter. Nun verhält es sich so, dass *S. cinerea* nach allem zu urteilen aus einer *viminalis* × *caprea*-Kreuzung entstanden ist; die triploide Rückkreuzung sollte also die gleiche Paarung wie die triploide (*viminalis* × *caprea*) gehabt haben. Wenn dies nicht der Fall war, hat dies vielleicht seine Erklärung darin, dass es in *cinerea* zu strukturellen Veränderungen gekommen ist. Sie hatten zur Folge, dass die beiden Genome von *cinerea* wahrscheinlich strukturell etwas verschieden sind, wenngleich nicht hinsichtlich aller sondern nur einem Teil der Chromosomen. Die Rückkreuzung von *S. cinerea* mit dem einen der Elternarten (*caprea*) zeigte eine besonders stark herabgesetzte Trivalentbildung. Während also *S. neocinerea* eine Autopolyploide mit zwei strukturell gleichen Genomen war, schien *S. cinerea* allopolyploid zu sein, und es verhält sich offenbar so, dass das letztere Stadium aus dem ersten hervorgegangen ist.

Die in den triploiden Bastarden vorkommenden Trivalente sind offenbar aus zwei *cinerea*-Chromosomen und einem von der diploiden Elternart gebildet. Die Bivalente wiederum können durch Allosyndese oder auch durch Autosyndese zwischen zwei *cinerea*-Chromosomen entstanden sein. Alle Univalente brauchen also nicht *cinerea*-Chromosomen zu sein. Die Bivalente des pentaploiden (*cinerea* × *phylicifolia*)-Bastarden können allo- oder autosyndetisch gebildet sein; wahrscheinlich kommen beide Arten von Konjugation vor.

Die grosse Sterilität der weiblichen Sträucher der *cinerea*-Bastarde

beruht nicht nur auf Störungen im Verlauf der Meiosis sondern steht vermutlich auch im Zusammenhang mit der in den Samenanlagen aller *cinerea*-Bastarde vorkommenden Verspätung der Teilung der Embryosackmutterzelle. Alle *Salix*-Bastarde, bei denen eine Verspätung festgestellt worden ist, sind stark steril gewesen, während bei mehr fertilen Typen die Meiosis normal eintrifft. Dies geht auch aus den Verhältnissen bei einer fertilen Form hervor, die aus einer stark sterilen solchen *Salix* entstanden ist. *S. laurina* ist ausserordentlich steril und ihre Meiosis, wie früher hervorgehoben, stark verspätet. Es ist jedoch gelungen von ihr Nachkommen zu erhalten, darunter eine vollständig fertile *S. superlaurina* (HERIBERT NILSSON, 1935). Bei dieser gibt es keine Verspätung, sondern die Meiosis 1 erfolgt zu normaler Zeit. Die Chromosomenzahl ist noch nicht definitiv bestimmt. Die Teilungen in der Embryosackmutterzelle verlaufen ohne Störungen.

SALIX [(PURPUREA × DAPHNOIDES) × (REPENS × AURITA)] × [(PHYLICIFOLIA × NIGRICANS) × (VIMINALIS × CAPREA)].

Dieser Bastard ist neulich beschrieben worden (HERIBERT NILSSON, 1937). Er soll Chromosomen von acht verschiedenen Arten enthalten. Der Bastard ist fertil und da sowohl männliche wie weibliche Sträucher erhalten worden sind, konnte eine grosse F_2-Generation aufgezogen werden. Vom 8-Bastarden selbst gab es jedoch nur fünf Sträucher (l. c.).

Die zytologische Untersuchung stiess auf gewisse Schwierigkeiten. Ein Strauch blühte nicht und gab auch im Wasser keine Wurzeln, die übrigen gaben allerdings Wurzeln, aber die Kernplatten waren sehr schlecht fixiert. Der am besten studierte war ein männlicher Strauch, entstanden aus einer Kreuzung, in der der diploide Elternbastard als Mutterpflanze fungierte.

Die Chromosomenzahl dieses Strauches konnte in somatischen Platten bestimmt werden. Sie betrug ungefähr 76 (Fig. 9 *a*). Der Strauch ist also tetraploid. Die Reduktionsteilung verlief sehr regelmässig. Sowohl während der Anaphase 1 (Fig. 9 *e*) wie während der Anaphase 2 konnten nur sehr selten zurückgebliebene Chromosomen beobachtet werden. Die Pollentetraden waren auch regelmässig und der Gehalt an schlechtem Pollen unbedeutend. Die Chromosomenpaarung konnte nicht näher analysiert werden. In den anscheinend am besten fixierten Metaphasenplatten wurden 35—36 oder ca. 38 Chromosomen gezählt. Hier sollten also fast nur Bivalente gebildet worden

sein (Fig. 9 *d*). Und auch in längsgeschnittenen Metaphasen 1 waren Multivalente selten zu sehen. Häufig konnte eine bedeutend geringere Anzahl Chromosomen gesehen werden, aber wahrscheinlich hat eine ungünstige Fixierung Zusammenballungen verursacht. Wir finden also, dass dieser Strauch eine Meiosis hat, die ungefähr der von *viminalis* × *phylicifolia* ähnlich ist, wahrscheinlich jedoch mit dem Unterschied, dass die Multivalentbildung etwas ausgeprägter ist. Das Zählen

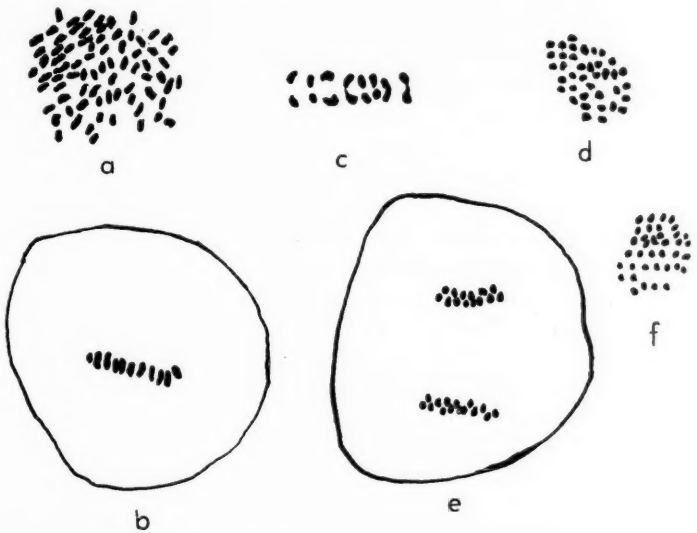


Fig. 9. *S. octogena* = *S.* [(*purpurea* × *daphnoides*) × (*repens* × *aurita*)] × [(*phylicifolia* × *nigricans*) × (*viminalis* × *caprea*)]. — *a*: Somatische Kernplatte. — *b*: M 1. — *c*: Bivalente. — *d*: M 1 quergeschnitten. — *e*: A 1. — *f*: A 1 Kernplatte.

der Chromosomen in den Anaphase 1-Platten war nicht leicht, es wurden jedoch Platten mit etwa der tetraploiden Zahl beobachtet (Fig. 9 *f*).

Ein Geschwisterstrauch zu diesem war intersexuell. Die somatische Chromosomenzahl konnte hier nicht bestimmt werden. Die Meiosis konnte in Pollen- und Embryosackmutterzellen studiert werden, hinsichtlich der ersteren auch in Antheren, die sich in den Fruchtknoten entwickelt haben. Die Chromosomenzahl konnte auch während der Meiosis nicht konstatiert werden, war aber ungefähr tetraploid. Die Chromosomenpaarung schien hier recht variierend. Häufig sind ein oder mehrere Univalente zu sehen, ausserdem konnten Multivalente vorkommen. Die Pollenfertilität war nicht vermindert.

DIE CHROMOSOMENPAARUNG BEI SALIX-BASTARDEN.

Alle untersuchten diploiden Artbastarde zeigten normale Chromosomenpaarung mit meistens 19 Bivalenten in der Metaphase 1. Die Genome in den verschiedenen Arten scheinen also strukturell einander gleich zu sein. Jedenfalls sind vielleicht vorhandene Verschiedenheiten gering. Eine wenig erhöhte Tendenz zu Univalentbildung bei den Artbastarden im Vergleich zu den reinen Arten beruht vielleicht auf kleinere strukturelle Unterschiede. Auch ein Bastard aus vier verschiedenen Arten hatte eine regelmässige Paarung, was die grosse Ähnlichkeit der Genome des weiteren bestätigt.

Einige *Salix*-Arten sind polyploid, enthalten also mehrere Genome. *S. phylicifolia* ist hexaploid. Aber es ist sehr wahrscheinlich, dass die drei Genome dieser Art strukturell gleich sind. Der Bastard mit *S. viminalis* zeigt nämlich Autosyndese zwischen zwei der Genome, während die Chromosomen des dritten mit den *viminalis*-Chromosomen gepaart sind; nichts spricht aber dagegen, dass auch dieses mit den anderen beiden übereinstimmt. Eine andere hexaploide Art ist *S. nigricans*. Früher habe ich ihren Bastard mit *S. phylicifolia* untersucht (HÅKANSSON, 1933). Dieser zeigte vollkommen normale Paarung. Offenbar ist auch *S. nigricans* autopolyploid, hat drei strukturell gleiche Genome, die ihrerseits mit dem Grundgenom von *S. phylicifolia* übereinstimmen.

S. cinerea ist die einzige bekannte tetraploide Art. Es ist früher erwähnt worden, dass sie wahrscheinlich aus einer Kreuzung zwischen *S. viminalis* × *caprea* entstanden ist. Die beiden Genome sollen also strukturell gleich sein. Eine Untersuchung der Artbastarde zeigte jedoch, dass wahrscheinlich gewisse Veränderungen stattgefunden haben. Sich bestimmt darüber auszusprechen ist ja schwierig, da die Bastarde tri- oder pentaploid sind und daher ziemlich variierende Paarungsverhältnisse in der Meiosis aufweisen. Hierzu kommt, dass fast nur weibliche Sträucher untersucht werden konnten. Es ist indessen offenbar, dass die Anzahl Univalente bei den triploiden Bastarden unerwartet gross ist, wenn wir die Meiosis mit der bei triploider *S. viminalis* × *caprea* vergleichen, was zweifellos darauf deutet, dass zwischen den beiden *cinerea*-Genomen strukturelle Unterschiede bestehen.

Eine Multivalentbildung ist in den tetraploiden Formen nicht häufig. So waren Quadrivalente selten bei *S. neocinerea* und *S. viminalis* × *phylicifolia*, etwas häufiger waren sie im 8-Bastard. Bei triploiden Typen wurden dagegen leicht Trivalente gebildet. Die untersuchte Pentaploide zeigte auch eine gewisse Multivalentbildung

Der Verlauf der Anaphase 1 und 2 zeigt bei den *Salix*-Bastarden Verschiedenheiten. Bei einem Teil sind diese Teilungen regelmässig und zurückgebliebene Chromosomen können nur selten beobachtet werden. In anderen Fällen waren sie von starken Störungen begleitet, was auch zur Bildung von Zwergpollenkörnern hat führen können. Die Anzahl von Chromosomen scheint für den Verlauf der Teilungen entscheidend zu sein. Bisher habe ich bei keinem diploiden Bastarden unregelmässige Teilungen gefunden, auch wenn derselbe vier verschiedene Arten enthielt. Ähnlich verhielt es sich mit den tetraploiden Bastarden. Sowohl bei *S. viminalis* × *phylicifolia* wie beim 8-Bastarden waren sie regelmässig wie bei den reinen Arten. Ich habe auch einige hexaploide Bastarde untersucht, obgleich ich meine Funde noch nicht veröffentlicht habe. Auch bei diesen waren Anaphase 1 und 2 regelmässig.

Störungen traten dagegen in sehr ausgesprochenem Grad bei tri- und pentaploiden Typen auf. Sowohl in den untersuchten *S. cinerea*-Bastarden wie in den triploiden *S. viminalis* × *caprea* und in *S. laurina* (pentaploid?) wurden gewöhnlich zurückgebliebene Chromosomen in der früheren Anaphase 1 wie auch in Anaphase 2 beobachtet. Eine aneuploide *Salix* zeigte gleichfalls Störungen (siehe S. 10). Es ist das Vorkommen von univalenten und trivalenten Chromosomen, das die Störungen in der Anaphase 1 verursacht: Die Univalente werden häufig längsgeteilt, die Separation der Chromosomen in einem Trivalent ist oft etwas verzögert, eines der Chromosomen in einem Trivalent kann längsgeteilt werden. Die Chromosomen, die während der ersten Teilung geteilt worden sind, werden dann offenbar während der zweiten nicht geteilt, was zur Folge hat, dass auch die Anaphase 2 einen unregelmässigen Verlauf bekommt.

SUMMARY.

The cross *Salix viminalis* × *caprea* was investigated cytologically. The two parent species are diploid, about one per cent of the F_2-shrubs are, however, triploids (♂ and ♀). At metaphase 1 of the triploids there are tri-, bi- and univalent chromosomes, the tendency to form trivalents is rather strong, and is stronger in male than in female shrubs. Anaphase 1 and 2 are irregular.

In F_2 there was also a shrub very similar to the tetraploid species *S. cinerea* (see HERIBERT NILSSON, 1931). This shrub was tetraploid, had a regular meiosis, and an embryo-sac (fertile) was formed in most

of the ovules. At metaphase 1 the tendency to form multivalents is weak. There were often only bivalent chromosomes, frequently, however, a few (1—3) multivalents could be observed.

The cross 2X × 3X was investigated. There were three triploid, two diploid shrubs and one aneuploid shrub, the latter had 2n = 41 chromosomes and an irregular meiosis.

The diploid hybrids *S. purpurea* × *hastata*, *S. aurita* × *hastata*, *S. repens* × *viminalis*, *S. viminalis* × *aurita* and *S. viminalis* × *daphnoides* had 19 bivalents at metaphase 1 and a regular anaphase 1 and 2.

The diploid hybrid *S.* (*purpurea* × *daphnoides*) × (*repens* × *aurita*) also had regular meiotic divisions and mostly 19 bivalents.

The hybrid between the diploid species *S. viminalis* and the hexaploid *S. phylicifolia* was tetraploid (n = 38). Meiosis is very regular, as in a tetraploid species. At metaphase 1 there are very often 38 bivalents, more seldom one or more multivalents could be observed. Presumably one of the genomes from *S. phylicifolia* pairs with the genome from *S. viminalis*, the chromosomes of the other two genomes from *S. phylicifolia* pairing autosyndetically. Structurally, the species *S. phylicifolia* must be an autohexaploid.

A hybrid between eight different *Salix*-species was investigated. This hybrid had arisen through crossing the diploid *S.* (*purpurea* × *daphnoides*) × (*repens* × *aurita*) and the tetraploid *S.* (*phylicifolia* × *nigricans*) × (*viminalis* × *caprea*) (see HERIBERT NILSSON, 1937). Two shrubs were found to be tetraploid. The meiotic divisions were very regular, lagging chromosomes being but infrequently seen. The chromosome pairing at metaphase 1 often resulted in only bivalents, but frequently some multivalents and univalents were formed.

Several hybrids between the tetraploid *S. cinerea* and other species were studied. *S. repens* × *cinerea*, *S. viminalis* × *cinerea*, *S. caprea* × *cinerea*, *S. aurita* × *cinerea*, *S.* (*viminalis* × *caprea*) × *cinerea* were triploid. They had an irregular meiosis, chromosome lagging in first and second division. At metaphase 1, trivalents, bivalents and univalents were seen, the percentage of trivalents was rather low. In some hybrids most of the chromosomes from one of the *cinerea*-genomes are probably unpaired, but more than 19 univalents were found at early anaphase only. The hybrid *S. cinerea* × *phylicifolia* was pentaploid and had also an irregular meiosis. Metaphase 1 had rather few multivalents but many univalents.

The meiotic divisions were greatly delayed in the ovules of the female shrubs of all the *cinerea*-hybrids. When the sterile tissue of

the ovules is fully developed, and should contain a mature embryo-sac, meiosis occurs. The female shrubs are very sterile. Only in *S. cinerea* × *phylicifolia* did embryo-sacs develop to maturity. In *S. purpurea* × *cinerea*, the nucleus of the embryo-sac mother cell never divided.

ZITIERTE LITERATUR.

1. FAGERLIND, F. 1937. Embryologische, zytologische und bestäubungsexperimentelle Studien in der Familie *Rubiaceæ* nebst Bemerkungen über einige Polyploiditätsprobleme. — Acta Horti Bergiani, 11.
2. FEDERLEY, H. 1931. Chromosomenanalyse der reziproken Bastarde zwischen *Pygæra pigra* und *P. curtula* sowie ihre Rückkreuzungsbastarde. — Zschr. f. Zellforsch. u. mikrosk. Anatomie, 12.
3. HÅKANSSON, A. 1929. Die Chromosomen in der Kreuzung *Salix viminalis* × *caprea* von HERIBERT NILSSON. — Hereditas XIII.
4. — 1933. Die Konjugation der Chromosomen bei einigen *Salix*-Bastarden. — Hereditas XVIII.
5. JÖRGENSEN, C. A. 1928. The experimental formation of heteroploid plants in the genus *Solanum*. — Journ. of Genetics, 19.
6. LEVAN, A. 1937. Chromosome numbers in *Petunia*. — Hereditas XXIII.
7. LILJENFELD, F. A. 1936. Karyologische und genetische Studien an *Fragaria*. II. Ist *Fragaria elatior* eine autopolyploide Pflanze? — Jap. Journ. of Botany, 8.
8. MÜNTZING, A. 1930. Outlines to a genetic monograph of the genus *Galeopsis*. — Hereditas XIII.
9. — 1932. Cyto-genetic investigations on synthetic *Galeopsis Tetrahit*. — Hereditas XVI.
10. — 1936. The evolutionary significance of autopolyploidy. — Hereditas XXI.
11. — 1937. The effects of chromosomal variegation in *Dactylis*. — Hereditas XXIII.
12. NILSSON, HERIBERT. 1918. Experimentelle Studien über Variabilität, Spaltung, Artbildung und Evolution in der Gattung *Salix*. — Lunds Univ. Årsskrift, N. F., Avd. 2, 14.
13. — 1930. Synthetische Bastardierungsversuche in der Gattung *Salix*. — Lunds Univ. Årsskrift, N. F., Avd. 2, 27.
14. — 1931. Über das Entstehen eines ganz *cinerea*-ähnlichen Typus aus dem Bastard *Salix viminalis* × *caprea*. — Hereditas XV.
15. — 1935. Die Analyse der synthetisch hergestellten *Salix laurina*. — Hereditas XX.
16. — 1937. Ein oktonärer, fertiler *Salix*-Bastard und seine Deszendenz. — Hereditas XXII.
17. NORDENSKIÖLD, H. 1937. Intra- and interspecific hybrids of *Phleum pratense* and *P. alpinum*. — Hereditas XXIII.

18. OVEREEM, C. VAN. 1921. Über Formen mit abweichender Chromosomenzahl in *Oenothera*. — Beih. Bot. Zentralblatt, 39.
19. RANDOLPH, L. F. 1932. Some effects of high temperature on polyploidy and other variations in maize. — Proc. Nat. Acad. Sc., 18.
20. SHIMOTOMAI, N. 1933. Zur Karyogenetik der Gattung *Chrysanthemum*. — Journ. sc. Hiroshima University, B. 2, 2.

INHALT.

Seite

Salix viminalis × *caprea*, F_2 2
Salix viminalis × (*viminalis* × *caprea*, triploid) 9
Einige diploide Bastarde 11
Salix (*purpurea* × *daphnoides*) × (*repens* × *aurita*) 14
Salix viminalis × *phylicifolia* 15
Salix cinerea-Bastarde 19
Salix [(*purpurea* × *daphnoides*) × (*repens* × *aurita*)] × [(*phylicifolia* × *nigricans*) × (*viminalis* × *caprea*)] 26
Die Chromosomenpaarung bei *Salix*-Bastarden 28
Summary 29
Zitierte Literatur 31

STUDIES ON THE GENETIC BASIS OF CHLOROPHYLL FORMATION AND THE MECHANISM OF INDUCED MUTATING

BY *ÅKE GUSTAFSSON*
INSTITUTE OF GENETICS, SVALÖF, SWEDEN

I. INTRODUCTION.

As far as I am aware, no close genetic study has yet been made of the physiological organisation in a plant or animal species, at any rate the properties of the manifold genes which determine the organisation have not been grouped and compared. One of the purposes of the present paper is to show the possibility of such a grouping and a regular aberration of segregation in certain *groups* of genes. Of the numerous genes which condition the formation of chlorophyll, some of them — with a definite phenotypic effect — behave genetically differently from other factors with quite different phenotypical effects. In spite of their different location in the chromosomes, genes (or gene blocks) with the same phenotypic effect thus possess a similar structure.

In three previously published papers I have investigated the direct effect of X ray irradiation on chromosomes and nuclei. In the present paper I present the results of an initial investigation of its genetic effect. In my first paper I believe I succeeded in demonstrating a varying degree of stability in the chromosomes according to different environments (water content and age) and the possible connection of the mechanism of reproduction with this stability. In the second paper some results were given of the chromosome stability and chromosome fusion in series of seeds, which had been treated with water before irradiation. The nuclei which first enter mitosis show intense fragmentation, and this formation of fragments in the earliest nuclei is increased in the same measure as the water content increases. The mechanism of reproduction was therefore regarded to be to a certain extent dependent on the water content of the nucleus. In my third paper it was shown that the nuclei of the cells died after irradiation in accordance with a definite law. Certain groups of nuclei were especially sensitive, showed a high frequency of chromosome disturbances and died more easily than others. One of the results of this work is the

genetic demonstration of a regularity in the death of the nuclei and that mutations of a certain type — macromutations of *alboviridis* — arise in those nuclei which show the highest frequency of chromosome disturbances and which at the same time die most easily.

In conclusion I wish here to express my gratitude to Prof. H. NILSSON-EHLE, Svalöf, for the kindness he has shown me during the execution of this series of tedious and extensive experiments and for the staff of assistants he placed at my disposal. To Dr. O. TEDIN, Svalöf, with whom I have discussed these experimental series, I wish to convey my thanks for valuable suggestions and criticisms. Grants have been made to me for the purpose of carrying out the investigations by Fysiografiska Sällskapet, Lund, and Längmanska Kulturfonden, Stockholm.

II. MATERIAL AND METHODS.

Like the previous investigations the present studies are mainly based on induced changes in resting caryopses of Gullkorn (Golden Barley). The technique employed in irradiating the so-called I—V series has been described in an earlier paper. The so-called VI series were irradiated on the 16th March 1936 in two stages with 96 kV and 2,5 m. a., all series for a period of 2 hours. Seed samples of both the 1934 and 1931 A and B Series were treated with water for 3 hours the day before irradiation. The 1934 A VI 3 h. and dry Series were placed in the said order in box No. 3 a (see 1937 a), the 1931 A VI 3 h. and dry in box No. 3 c, while the 1934 B VI 3 h. and dry were placed in box No. 2 a and the 1931 B VI 3 h. and dry in box No. 2 c. In the experiments with the VIII Series the ordinary X ray tube was not employed, a tube fitted with a Lindeman window for the production of long wave rays being used instead. In these experiments the boxes were only $6{,}5 \times 8$ cm. in size and the distance from the anticathode to boxes Nos. 2 a and 2 b as well as to boxes Nos. 3 a and 3 b was 20 cm. The voltage was 25 kV and the intensity of the current 10 m. a. The period of irradiation in all cases was $2\,^1/_2$ hours. The 1935 A VIII Series were placed in box No. 2 c, the 1935 B VIII Series in box No. 2 a, the 1932 A VIII Series in box No. 3 c and the 1932 B VIII Series in box No. 3 a. The irradiation was carried out on the 21st April 1936. The seeds of the III—VIII Series were sown on the 7th—8th May 1936.

In addition to these numbered series, 1935 caryopses of certain green homozygotes of Gullkorn mutations, 1934 homozygous green caryopses of these mutational lines as well as caryopses of heterozygous plants from these mutational lines and of heterozygotes and green homozygotes of the mutational lines *albina* 1, 2 and 3 and *xantha* 1 and 2 were irradiated. In 1934 the position of the series at the X raying was not noted in accordance with the method subsequently employed, only the period of irradiation and the distance from the anticathode being recorded. The heterozygous seeds of *albina* 1, 2 and 3 were irradiated for 105, 120 and 90 minutes respectively at a distance of 24, 25 and 30 cm. respectively from the anticathode. The heterozygous seeds of *xantha* 1, 2 and 3 were irradiated for 105, 105

and 130 minutes at a distance of 25, 23 and 26 cm. from the anticathode. The heterozygous seeds of *alboxantha* (2 samples) were X rayed for 120 and 135 minutes respectively at a distance of 30 and 31 cm. respectively. The sequence of these heterozygotes in respect to irradiation should be approximately the following: *Albina* 2, *xantha* 3, *xantha* 2, *albina* 1, *alboxantha* 1, *xantha* 1, *alboxantha* 2 and finally *albina* 3.

Of the mutations recorded in Table 8, *alboviridis* X 1 was obtained from *albina* 1 (homozygote), *alboviridis* X 2 from *albina* 2 (homozygote), *albina* X 1 from *albina* 3 (homozygote), *albina* X 2 from *alboxantha* (homozygote), *xantha* X 1 and X 2 from respectively *albina* 1 (homozygote) and *alboxantha* (homozygote).

All the mutations included in Tables 1 and 2 are derived from Gullkorn and from the above-named mutational lines from it. The material from the irradiation of the other mutational lines is not large enough to determine line differences with regard to mutation frequencies but the fragmentary figures seem to show that the frequency of induced mutations and the percentage of the different types of mutations are not only determined by age, water content, X ray dosage, etc., but also by the genotype of the irradiated mother line.

In the experiments, carried out in 1935 and 1934, also broken ears of progenies of irradiated caryopses were put to germinate, for the purpose of determining mutations, unfortunately without recording the number of plants having only one ear. For that reason it has not afterwards been possible for me to distinguish between plants with one ear and those ears which had broken off when harvested, the mother plant of which is not known. On that account all plants with one ear and the broken ears have been excluded in the mutation rate determinations of 1934 and 1935. The small differences in the frequency of mutations for the I Series in Table 7 in my paper 1937 b and for those in Table 9 below are due to this omission. The most extensive material originated from the 1936 experiments and in these all broken ears have been eliminated.

The induced chlorophyll mutations, like the spontaneous, in barley may be conveniently divided into five phenotypic groups: *albina*, *xantha*, *viridis*, *alboviridis* and *tiger*. The boundaries between the five groups are of course difficult to define exactly, this is especially true of the two groups *xantha* and *viridis*. In *xantha* there exist types ranging from sulphur-yellow to those in which the yellow ground colour has a more or less pronounced greenish tinge. Transitional types may also occur between *xantha* and *albina*. Such a mutation is mentioned on p. 56, which has rather hesitatingly been referred to *xantha*. The *albina* 530 mentioned by SCHICK and STUBBE (1932) is probably another intermediate form, which should be placed among the *xantha* types.

The *alboviridis* and *tiger* groups may be called *composite* groups in contradistinction to the other three groups. Of spontaneous mutations, I refer the mutation *alboxantha* (NILSSON-EHLE) to the *alboviridis* group. This mutation is deep yellow but at the apex displays a sudden change from yellow to white or whitish yellow. Thus mutations in which the apex and the base of the leaves have different colours belong to this group. The commonest mutation in this group has a long white base with a green apex. Another type has a yellow base and a yellowish green—green apex. Of the types mentioned on p. 60, *alboviridis* X 2 is white with a green apex, *alboviridis* X 1 yellow with a green apex. The so-called *tiger* type, which has not yet been obtained spontaneously, arose the first time in NILSSON-EHLE's X ray ex-

periments (unpublished), but has since occurred in almost the same appearance several times in my investigations. It is characterised by alternate transverse streaks of brown and yellowish green, where the brown parts in withering become pinched in. In the majority of cases these mutations are more or less dwarfish with narrow, greatly involute laminae. Yet some mutations with unfolded laminae and probably with a certain capacity of assimilation have appeared.

These rather easily phenotypically identifiable groups of mutations show themselves, according to my investigations, to correspond to definite genic or chromosomal characters, and thus there exists a parallelism between phenotypic and genotypic characters. It is noteworthy that the phenotypically extreme types in both the simple and composite groups of mutations involve, from a genetic point of view, the least changes, while *xantha*, *viridis* and *alboviridis* give rise to intense disturbances in the course of segregation, and of those *alboviridis* moreover is frequently due to chromosome disturbances. This parallelism between phenotypic and genetic characteristics seems to me to be very interesting from a phylogenetic point of view. Possibly the different groups of chlorophyll genes are inherently composed of similarly built genes, which therefore have a common and identical origin. Table 6 shows that this parallelism between phenotypic and genotypic characteristics is probably true not only of my material but is met with in great parts of the plant system.

In addition to these five main groups of mutations isolated divergent types of mutations are formed. The so-called *striata* mutations belong to this category, although none has so far been obtained in my material. An induced mutation which has now been studied in the fourth generation differs from the rest in that the gene (?) in question causes a sectorial division of the laminae into green and white longitudinal striations, which are as wide at the base as at the tip and which therefore indicate a definite regularity during the ontogenesis with respect to the inactivation of the chloroplasts. The segregation is 3 : 1, but with a deficiency of recessives, which is no doubt associated with the fact that the white parts vary in intensity, so that extreme white and extreme green recessives occasionally arise.

The so-called V Series have been excluded from Tables 9 and 10 below, as they have probably been confused with each other. They show quite the opposite conditions to those expected, not only with respect to the frequencies of mutations, mutated zygotes and types of mutations but also as regards percentage of germination, percentage number of full-grown plants as well as number of seeds per ear (this varies to a certain extent in proportion to the water content of the caryopses). On the other hand, the mutations obtained in these series have been included in Tables 1 and 2, where a mistake in labelling is of no consequence.

In estimating the frequencies of mutations, etc. for the various series only one half of each ear of all plants was put to germinate. Later in the field trials, the other half of those ears in which one or more mutations occurred was put to germinate. In this way it was possible to determine the frequency of mutations and the type of mutation quickly and reliably while at the same time it was possible to preserve the induced mutations — at least in those cases where they consisted of micromutations.

III. THE GENETIC BASIS OF CHLOROPHYLL FORMATION.

1. THE RANGE OF THE INDUCED CHLOROPHYLL MUTATIONS.

In a previous paper (1937 b, p. 19) it was shown that *albina* mutations appear with a greater number of individuals per mutation than other mutational types. This circumstance was interpreted in such a way that the *albina* mutations were on the average correlated with minor changes in the genotype and that they were not subjected to the same extent as the other mutations to selection during ontogenesis. This explanation was supported by other results, among others, by the different frequencies of the mutations in the oldest irradiated series. No distinction was made between the different types in the non-white group.

TABLE 1. *The Number of Mutations with 1, 2 and >2 Individuals/Mutation.*

Type of Mutation	Mutations with 1 Ind.	Mutations with 2 Ind.	Mutations with >2 Ind.	Σ
Albina	118 = 48,2 %	71 = 29,0 %	56 = 22,9 %	245 = 47,7 %
Xantha	42 = 53,8 %	21 = 26,9 %	15 = 19,2 %	78 = 15,2 %
Viridis	54 = 62,1 %	23 = 26,4 %	10 = 11,5 %	87 = 16,9 %
Tiger	13 = 56,5 %	3 = 13,0 %	7 = 30,4 %	23 = 4,5 %
Alboviridis	51 = 63,0 %	18 = 22,2 %	12 = 14,8 %	81 = 15,8 %
Σ	278 = 54,1 %	136 = 26,5 %	100 = 19,5 %	514

In subsequent fertility investigations altogether 514 mutations were examined. The number of *albina* mutations amounts to 48 per cent (Table 1). These mutations are three times more common than the *xantha*, *viridis* or *alboviridis* types, and about 10 times more frequent than the *tiger* type, which is the rarest of the chlorophyll mutations. Although the various *albina* mutations have not yet been investigated in respect to linkage, their numeral superiority is certainly not due to a higher degree of lability in the genes (in those cases in which the mutations are caused by a gene change), but to the fact that the *albina* genes are more numerous than other chlorophyll genes. This is in fact in accordance with the frequency of various spontaneous types of mutations in barley (cf. maize, DEMEREC, 1935 a, p. 81, and EYSTER, 1934, p. 233).

Table 1 shows the range of the different mutations in the individual ears. The *albina* types occur also here more extensively than the other mutations with 2 and 3 individuals. The difference between

albina and the total number of the mutations in this respect amounts to $\chi^2 = 6{,}612$ with a corresponding P value of about 0,01, which is quite significant. The *tiger* types are included among the non-*albina* mutations (see below).

A differentiation of the material in the various types reveals interesting differences. Mutations consisting of 1 individual occur in *albina* in 48 per cent of the cases, in *xantha* in 54 per cent, in *viridis* in 62 per cent and in *alboviridis* in 63 per cent. In *tiger* the percentage lies between that of *xantha* and *viridis*, i. e. at 57 per cent. The difference between *white* and *yellow* and between *white* and *tiger* is not significant, on the other hand the difference between *white* and *green* ($\chi^2 = 4{,}975$) and between *white* and *alboviridis* ($\chi^2 = 5{,}330$) is significant.

The column of mutations containing 3 or more individuals per ear shows the same relations. The percentage of *tiger* has, however, increased considerably. The sequence of the five types of mutations is: *tiger*, *albina*, *xantha*, *alboviridis* and *viridis*. The differences between *white* and *yellow* and between *white* and *alboviridis* are not significant, whereas the difference between *white* and *green* ($\chi^2 = 5{,}211$) is significant. The differences between *tiger* on the one hand and *white*, *yellow* and *alboviridis* on the other hand are not significant, but the difference between *tiger* and *green* ($\chi^2 = 5{,}012$) is significant.

The results recorded in my earlier paper have thus been confirmed. *Albina* (and *tiger*) show a higher percentage of minor mutations (below called micromutations) than *xantha*, and the last-mentioned in turn a higher percentage than *viridis* and *alboviridis*. *The sequence of the five types of mutations will therefore be*: (*albina* → *tiger*) → *xantha* → (*viridis* → *alboviridis*).

2. THE FERTILITY OF EARS WITH INDUCED CHLOROPHYLL MUTATIONS.

Assuming that the previous results can be interpreted as I have suggested, two kinds of mutations must exist in the second generation after irradiation in spite of the vigorous selection during ontogenesis: *macromutations*, for the most part chromosome structurally conditioned or at any rate structurally correlated, and *micromutations*, which are not structurally correlated and therefore able to comprise more individuals per mutated ear or plant. This division is purely descriptive. The macromutations are not genically conditioned, or at any rate genically + structurally conditioned, whereas the micromutations may well consist of genic changes. The macromutations need not have arisen as a

direct result of the X ray irradiation but may be caused ultimately by structural changes in the chromosomes and be produced from them by disturbances at meiosis. The micromutations, on the other hand, must, at any rate when they consist of many individuals (for instance, 4 mutants[1] of 8—10 individuals in an ear), have arisen at such an early stage of ontogenesis that already when meiosis sets in they are actual changes in the genotype.

The macromutations, caused to a greater or smaller extent by structural changes in the chromosomes, should on that account be attended by a certain degree of sterility. The ears, in which these macromutations appear, should on the average be characterized by a lower number of individuals than the non-mutated sister ears and those ears in which micromutations appear. It might be expected that ears without mutations would purely by chance show a smaller number of individuals than ears with one mutated individual and that the latter in turn would show a lower number of individuals than ears with two or more mutated individuals. The postulated sterility in ears with one mutated individual should thus be counterbalanced by the chance increase in the number of individuals, which must occur in order to realize the chance of finding one mutated individual.

The results recorded in Table 2 have therefore been obtained in the following manner. In those cases in which one or

[1] In this paper I designate as mutant the solitary mutated individual; mutation, on the other hand, denotes the type of mutation. A mutation may thus consist of one or more mutants.

TABLE 2. *The Fertility of Ears Containing 1, 2 and > 2 Individuals/Mutation.*

1	2	3	4	5	6	7	8	9	10	11
Type of Mutation	Number of Individuals per Ear				Diff. 2—5	D/m	Diff. 3—5	D/m	Diff. 4—5	D/m
	1 mut. Ind.	2 mut. Ind.	> 2 Ind.	Normal Ears						
Albina.....	6,85 ± 0,18	7,47 ± 0,26	8,03 ± 0,21	7,20 ± 0,09	— 0,35 ± 0,21	1,67	0,27 ± 0,28	0,96	0,83 ± 0,23	3,61
Xantha ...	6,90 ± 0,30	6,95 ± 0,59	7,94 ± 0,55	7,40 ± 0,14	— 0,50 ± 0,33	1,51	— 0,45 ± 0,61	0,74	0,49 ± 0,57	0,86
Viridis.....	6,98 ± 0,31	7,87 ± 0,46	7,70 ± 0,54	7,17 ± 0,13	— 0,19 ± 0,34	0,56	0,70 ± 0,48	1,46	0,53 ± 0,55	0,96
Tiger	6,23 ± 0,62	7,67 ± 0,33	7,86 ± 0,60	6,50 ± 0,30	— 0,27 ± 0,69	0,39	1,17 ± 0,45	2,60	1,36 ± 0,66	2,06
Alboviridis	6,26 ± 0,35	7,11 ± 0,50	8,38 ± 0,54	7,14 ± 0,15	— 0,88 ± 0,38	2,32	— 0,03 ± 0,53	0,06	1,24 ± 0,56	2,21

more mutants appeared in an irradiated plant progeny, a record was made of the number of mutated and normal individuals in the mutated ear and the number of individuals in the non-mutated sister ears (from the same plant). A classification of this material should thus present a good picture of the conditions of fertility. Only mutated plants containing at least two ears have been included in the table. Several mutations have therefore been excluded. The total number of mutations examined amounts to more than 600. In this table, as in the preceding, 514 mutations have been employed. The number of mutated ears is somewhat higher, for the same mutation may occur in two or more ears of the same plant. Both or all of these ears have therefore been included in the column of mutated ears.

The number of individuals in the normal ears have been obtained by adding all normal ears of the type of mutation in question. The average of the normal ears are: in *albina*, 1 mutated individual 7,17, 2 mutated individuals 7,28 and more than 2 mutated individuals 7,18, together 7,20; in *xantha*, 7,43, 7,64 and 7,19 respectively, together 7,40; in *viridis*, 7,00, 7,76 and 6,55 respectively, together 7,17; in *alboviridis*, 7,07, 7,29 and 7,29 respectively, together 7,14; in *tiger*, 6,66, 5,90 and 6,56 respectively, together 6,50. The three values differ slightly from one another (with the exception of *viridis*, see below). We are therefore justified in adding the normal ears together. Even if no combination is made, the final result will be the same, only the values of D/m being changed. The varying number of individuals in the five types of mutations is mainly due to differences in representation. The irradiated series of seeds show a greatly varying number of individuals per plant, due to the intensity of irradiation, number of plants in the plot, water content, age, etc. For this reason the values of the different types of mutations cannot be compared with each other.

In all groups, ears with 1 mutated individual show lower values of the number of individuals per ear than the normal sister ears, in spite of the fact that, from the point of view of chance, an increase might be expected. The five negative values of D/m are thus to be regarded as minimum numerical values. Their magnitude (1,67, 1,51, 0,56, 2,32 and 0,39 respectively) is in itself sufficient evidence of the sterility of the mutated ears. In two of the five groups, ears with two mutated individuals show negative differences (in *xantha* a D/m of 0,74 and in *alboviridis* a D/m of 0,06). The other three groups give highly positive differences with D/m values of 0,96, 1,46 and 2,60 respectively. Ears with at least three mutants show throughout positive differences with high

D/m values, 3,61, 0,86, 0,96, 2,21 and 2,06 respectively. If these fertility values are a measure of the genetic size of the mutation, then *xantha* and *alboviridis* must be caused by great changes in the genotype, *albina* and *tiger* by much smaller changes. As mentioned above, the values for *viridis* are not so reliable as those for the other types, for the number of individuals in the three groups of ears varied greatly, from 7,00, and 7,76 to 6,65 with an average of 7,17. — The average values of the three groups of D/m will be + 4,27 for *tiger*, + 2,90 for *albina*, + 1,86 for *viridis* (cf. above), — 0,17 for *alboviridis* and — 1,39 for *xantha*. These figures undoubtedly point in the same direction as those given previously.

TABLE 3. *The Correlation between the Position of Mutated Zygotes and Fertility.*

	A		B		C	
Type of Mutation Number of Mutants	Mutants quite close		Mutants partly separated		Mutants quite separated	
	Mutat. ears	Normal ears	Mutat. ears	Normal ears	Mutat. ears	Normal ears
Albina. 2 mutants...	8,50 ind./ear	8,03 ind./ear	7,33 ind./ear	7,25 ind./ear	6,67 ind./ear	7,50 ind./ear
	8,15 ind./ear		7,29 ind./ear		7,30 ind./ear	
Number of ears ...	10	30	6	14	9	24
Non-Albina. 2 mutants	8,14 ind./ear	8,08 ind./ear	—	—	7,33 ind./ear	7,91 ind./ear
	8,09 ind./ear		—		7,79 ind./ear	
Number of ears ...	7	25	—	—	6	23
3 or more mutants	8,08 ind./ear	7,16 ind./ear	7,85 ind./ear	7,35 ind./ear	9,50 ind./ear	7,17 ind./ear
	7,40 ind./ear		7,49 ind./ear		7,75 ind./ear	
Number of ears ...	12	33	13	32	2	6

Unfortunately the *exact* location of the mutants in the ears was not recorded until at the end of the investigation. Careful records were only made in the case of the so-called IV, V and VI Series. In 38 ears with 2 mutants per ear the location was noted exactly, the number of sister ears in this group amounts to 116. The corresponding figure for ears with 3 or more mutants is 27 and the number of sister ears is 71. In Table 3, column A denotes that the two mutated individuals are situated quite close to each other, column B that they are situated near each other, and column C that they are quite separated. Of the 38 mutations, 23 or 60 per cent are close to each other and can thus hardly be other than micromutations, while 15 or 40 per cent are quite separated from each other. Some of the mutations in this group are possibly macromutations. That this is the case is shown by a com-

parison between mutated and normal sister ears. Let us first consider the *white* mutations. Ears with 2 mutants situated quite close to each other have 8,50 individuals per ear as against 8,03 for the sister ears, ears with 2 mutants near each other, 7,33 as against 7,25, and finally ears with 2 entirely separated mutants, 6,67 as against 7,50. The contrast is striking. The *non-white* mutations show the same conditions: in Group A, 8,14 individuals per ear against 8,08, and in Group C, 7,33 individuals against 7,91. Although the differences are not statistically significant in any of the cases, they nevertheless confirm the results recorded previously. The total average of individuals per ear in the three columns is: 8,15 as compared with 7,29 and 7,30 for the *white* mutations, and 8,09 as compared with 7,79 for the *non-white* mutations. The group which might have been expected to contain the most macromutations also shows the highest rate of fertility — not only in the mutated ears but also in the unmutated.

Mutations comprising 3 or more mutants have been divided into 3 classes according to their relative location. Mutations with 3 individuals have been grouped as follows: in column A, mutations where all mutants are situated close to each other; in column B, mutations where 2 mutants are close to each other; in column C, mutations where the mutants are separated from each other. Mutations consisting of 4 individuals are grouped in the following manner: in column A, mutations with 4 or 3 mutants lying quite close to one another; in column B, mutations with 2 groups of mutants quite close to each other; in column C, mutations with at most 2 mutants close to one another. The number of mutations examined amounts to 25 (27 ears). The number of sister ears is 71. There are 11 mutations in group A, 12 in group B and 2 in group C. The rate of fertility differs considerably from that in the preceding case. The number of individuals in the mutated ears amounts to 8,08, 7,85 and 9,50 respectively, as compared with 7,16, 7,35 and 7,17 in the sister ears. All mutations consist here of micromutations, mutations which have not in any way disturbed the course of nuclear division or of life in the germinating seeds and the growing plants. The total average of individuals in the three classes amounts to 7,40, 7,49 and 7,75, thus no sterility occurs in class C.

It has thus been shown that the mutations formed in the second generation after the irradiation are divided into two groups. The first group consists of macromutations. These macromutations are attended by cytological complications with a slight but quite evident decrease in fertility in the mutated ear in consequence and occur only in single

individuals. They are probably not direct products of the irradiation but arise only secondarily, owing to induced cytological disturbances (inversions, translocations, duplications, etc.), which prevent the normal accomplishment of the zygotene pairing. Thus they may be nothing but deficiencies arisen meiotically. The second group, the micromutations, does not bring about any decrease in fertility and is therefore not correlated with cytological disturbances. These mutations must therefore have arisen as gene changes in the resting nuclei on irradiation or as a result of structural changes in the chromosomes during or shortly after irradiation. The possible structural changes, by means of which they arose, must, however, be so slight that they do not involve any changes in the regular accomplishment of meiosis. (There is of course nothing to prevent great structural changes in a genome from arising at the same time as the micromutation. In that case the micromutation, however, is independent of the structural change.)

The types of mutations are in varying degree macromutations. This is most pronounced in the case of the *xantha*, *viridis* and *alboviridis* types, less pronounced in the case of the *albina* and *tiger* types. In another connection (p. 69) it will be shown that of these types, *alboviridis* is the one most closely correlated with chromosome disturbances. *Alboviridis* mutations are therefore produced for the most part owing to cytological aberrations.

3. THE SEGREGATION CONDITIONS IN SPONTANEOUS CHLOROPHYLL MUTATIONS IN BARLEY.

In the preceding chapter it was shown that *albina* mutations are caused by or correlated with cytological changes in the chromosomes to a less extent than the other mutations. Still, a discontinuous transition between macromutations and micromutations hardly occurs. A certain minimum of structural aberration is necessary, however, before a marked decrease in fertility can ensue. In the same manner as there are transitions in the group of macromutations down to the border-line for the micromutations (p. 41, mutations with 2 mutants per ear), it is conceivable that similar differences in size also exist among the micromutations.

Of the 14 mutations analysed by HALLQVIST in 1924, one, *Zwerg* 1, shows an exceedingly great aberration of segregation. Such a great deficiency of recessives arises that the D/m amounts to 26,5. In addition to dwarfishness and gametic lethality this mutation is characterized

by changes in the chlorophyll formation (HALLQVIST, 1923). At low temperature the mutation will be yellowish white in colour, at a somewhat higher temperature it produces chlorophyll rather quickly and at a temperature above 30° C. almost immediately. It can thus be referred to the *viridis* group. HALLQVIST (1923) has been able to show that the divergent segregation is not due to want of vitality in the germinating caryopses, nor to the death of the zygotes in an early or late seedling stage but quite simply to a gamete elimination.

TABLE 4. *The Segregation of Spontaneous Chlorophyll Mutations in Barley* (HALLQVIST, 1924).

Type of Mutation	D/m	$\Sigma\chi^2$	P
Albina 3	0,93	0,867	—
» 4	0,44	0,195	—
» 5	0,14	0,021	—
	0,50	1,083	0,78
Xantha 1	0,95	0,891	—
» 2	0,47	0,217	—
	0,71	1,108	0,58
Virescens 1	1,90	3,607	—
» 2	1,28	1,633	—
» 3	1,79	3,216	—
	1,66	8,456	0,04
Lutescens 1	0,05	0,003	—
» 2	1,52	2,315	—
Chlorina	0,91	0,833	—
Superchlorina	0,25	0,062	—
	0,68	3,213	0,52
Linearis	0,77	0,597	—

Of the remaining 13 mutations, 3 consist of *albina*, 2 of *xantha*, 2 of *lutescens*, 3 of *virescens* and 2 of *chlorina* (see Table 4). The last 7 should be referred to the *viridis* group. None of *albina* 3, 4 or 5 shows a D/m value of over 1,00 (field experiments with *albina* 3 excluded, see HALLQVIST, p. 74), and none of *xantha* 1 and 2 whereas 4 of the 7 *viridis* types have D/m values above 1,00. The average D/m for *albina* is 0,50, for *xantha* 0,71 and *viridis* 1,06 (*linearis* included but not *Zwerg* 1). The differences are not significant but *albina* nevertheless shows the least deviations. A closer analysis confirms this fact.

$\Sigma\chi^2$ equals 1,083 for the three *albina* mutations with a corresponding

P value of 0,78, for the two *xantha*, 1,108 with a P value of 0,58, for the three *virescens*, 8,456 with a P value of 0,04, and for the remaining 4 *viridis* types (*linearis* and *Zwerg* 1 excluded), 3,213 with a P value of 0,52. Thus the three *virescens* mutations differ significantly from the others (with the exception of *Zwerg* 1), in that they certainly show a 3 : 1 segregation, but this is disturbed in some way or other. This is not due to an elimination of recessive zygotes, for in one of the cases — *virescens* 2 — there is an excess of recessives.

The progenies of 10 chlorophyll hetero- or homozygotes of barley are planted every year in the experimental fields at the Institute of Genetics, Svalöf (NILSSON-EHLE): *albina* 1, 2, 3, 7, *xantha* 1, 2, 3, *alboxantha*, *lutescens* and *chlorina*. All these mutations are spontaneous, *albina* 7, *xantha* 3, *alboxantha*, *lutescens* and *chlorina* obtained from Gullkorn (cf. NILSSON-EHLE, 1922). In the autumn of 1936 I made a careful analysis of the segregation ratios of the first 8 of these types. A comparison between *albina* and *xantha* in particular will be of value. Table 5 gives the segregation ratios and the value of D/m and χ^2. The average of D/m for *albina* is 0,86, for *xantha* 1,08. For *albina*, $\Sigma\chi^2$ is 3,249 with a P value of 0,51, for *xantha*, 4,699 with a P value of 0,20. Thus there is a marked difference also here.

The favourable segregation ratio of *xantha* 3 is only apparent, owing to two opposing tendencies in the sex cell (or zygote) formation. In examining the segregation families it was at once seen that progenies of plants with a large number of ears showed a deficiency of recessives as compared with plants with few ears. This observation was confirmed in the actual count. Five progenies of plants with 3, 4 and 5 ears segregated in the ratio of 329 : 134, that is showed a great excess of recessives. The D/m is 1,96. Five progenies of plants with more than 5 ears per plant gave the ratio of 606 : 174, that is an equally great deficiency. The D/m here is 1,74. The difference between the two groups of plant progenies amounts to $\chi^2 = 6{,}857$ with a corresponding P value of $< 0{,}01$.

Thus *xantha* 3 shows very great variations in the segregation numbers, in spite of the fact that the disturbances are antagonistic and counterbalance each other in the final result.

A similar classification of the other mutations reveals a very wide difference between *albina* and *xantha* in the group comprising plants having only a few ears. (The mutations originate from different basic material and consequently show variable averages of the number of ears per plant.) The average D/m for *albina* in the group with few ears

TABLE 5. *The Segregation of Spontaneous Chlorophyll Mutations in Barley.*

I.

Type of Mutation	Segregation	D/m	$\Sigma\chi^2$	P	
Albina 1	663 : 228 = 891	0,41	0,165	—	
» 2	846 : 264 = 1110	0,94	0,876	—	
» 3	744 : 229 = 973	1,05	1,113	—	
» 7	807 : 289 = 1096	1,05	1,095	—	
Σ		0,86	3,249	0,51	
Xantha 1	1352 : 415 = 1767	1,47	2,160	—	
» 2	362 : 101 = 463	1,58	2,507	—	
» 3	935 : 308 = 1243	0,18	0,032	—	
Σ		1,08	4,699	0,20	
Alboxantha	991 : 330 = 1321	0,02	0,000	—	

II.

Albina 1	434 : 148 = 582	0,25	0,057	—	3 + 4 + 5 ears / plant
» 2	522 : 177 = 699	0,20	0,039	—	2 + 3 »
» 3	357 : 110 = 467	0,70	0,520	—	2 + 3 »
» 7	172 : 59 = 231	0,19	0,036	—	3 + 4 + 5 »
Σ		0,34	0,652	0,96	
Xantha 1	596 : 175 = 771	1,49	2,180	—	2 + 3 + 4 »
» 2	210 : 55 = 265	1,60	2,547	—	2 + 3 »
» 3	329 : 134 = 463	1,96	3,836	—	3 + 4 + 5 »
Σ		1,68	8,563	0,04	
Alboxantha	473 : 146 = 619	0,81	0,660	—	3 + 4 + 5 »

III.

Albina 1	229 : 80 = 309	0,36	0,131	—	> 5 »
» 2	324 : 87 = 411	1,79	3,219	—	> 3 »
» 3	387 : 119 = 506	0,77	0,593	—	> 3 »
» 7	635 : 230 = 865	1,08	1,165	—	> 5 »
Σ		1,00	5,108	0,28	
Xantha 1	756 : 240 = 996	0,66	0,433	—	> 4 »
» 2	152 : 46 = 198	0,57	0,331	—	> 3 »
» 3	606 : 174 = 780	1,74	3.016	—	> 5 »
Σ		0,99	3,780	0,30	
Alboxantha	518 : 184 = 702	0,74	0,549	—	> 5 »
Σ *Albina* II + III	—	0,67	5,760	0,68	
Σ *Xantha* II + III	—	1,34	12,343	0,05	

per plant is 0,34, for *xantha* 1,68. The P values are 0,96 and 0,04 respectively. The segregation rate of *xantha*, taken collectively, lies outside the limits of 3 : 1.

In the group with several ears per plant a levelling takes place between *albina* and *xantha*, as shown by the D/m values. The average D/m value for *albina* is 1,00, for *xantha* 0,99. A great deficiency of recessives occurs in *albina* 2. On the other hand, *xantha* 1 and 2 are characterized by having a great deficiency of recessives only in the few-eared group. Such great contrasts between the two plant groups as in *xantha* 3 do not exist elsewhere. If the two groups of the differentiated material are added together, χ^2 for *albina* amounts to 5,760 ($P = 0,68$) and for *xantha* to 12,343 ($P = 0,05$).

From a theoretical point of view these results are of interest. *They show that the segregation ratios may vary quite considerably with the internal physiological characters of the mother plant* and that probably simple nutritional conditions have an influence on the formation of sex cells or on the vitality of the sex cells (or of the zygotes). (See further below).

In the spring of 1934 caryopses of several spontaneous chlorophyll heterozygotes were irradiated for the purpose of studying partly the linkage conditions of the newly arisen mutations, partly the location of the original chlorophyll genes in the induced double-heterozygotes. The segregation ratios in the progenies of the non-mutated plants were studied. It is to be expected that X ray irradiation will have a differential effect on the segregation, so that heterozygotes of mutations which, from a genetical point of view, involve the greatest changes in the genotype will be most easily disturbed in their segregation. That is also the case. If the segregation numbers of the irradiated heterozygotes are compared with those already given no differences will be seen in the *albina* mutations (χ^2 for *albina* 1, 2, 3 is 0,713, 0,623 and 0,020 respectively), while the differences in the case of the *xantha* mutations amount to 3,160, 16,493 and 0,099 respectively. If *xantha* 3 is divided into plants with 3, 4 and 5 ears and into plants with more than 5 ears, χ^2 will amount to 2,050 in the former case and to 2,210 in the latter. Two heterozygotes of *albo-xantha* were subjected to an unequal intensity of irradiation, and here, too, the corresponding differences are high (χ^2 equals 3,486 and 1,203 respectively). Although no great value as evidence can be attached to these series irradiated in 1934, they nevertheless confirm the results obtained previously.

This investigation has shown that *albina* mutations in barley in both HALLQVIST's material and my own exhibit fewer disturbances in the course of segregation than *xantha* and *viridis* mutations. The differences which have been studied most thoroughly are those between *albina* and *xantha*. The differences, which are too small to be assigned any value in ordinary numerical segregation analysis, have been made more pregnant by classifying the material according to the physiology

of the mother plant. This circumstance also shows that the numerical treatment of segregation ratios hitherto employed may conceal similar phenomena in many cases, and that an individual treatment of the progenies of the heterozygotes in other plants may furnish valuable results.

The present investigation carries the previous discussion a step farther. In the same manner as macromutations and micromutations are unevenly distributed among the mutational types, differences also exist between the normally or seemingly normally segregating micromutations. The type of mutation which gives the highest frequency of micromutations (*albina*), also shows the least disturbances in the course of segregation, in spite of the fact that the *albina* mutations are extreme types with the phenotypically greatest change in the apparatus of assimilation.

4. CHLOROPHYLL MUTATIONS IN OTHER SPECIES OF PLANTS.

Especially interesting are the induced mutations obtained in rice (KANNA, 1935). In that work the segregation numbers of 12 mutations are analysed, not so closely, it is true, as might be considered necessary in view of the results previously recorded. These 12 mutations may be divided into 4 groups. The first group comprises only the mutation *albinotic*, the second group contains the mutations *light cream*, *heavy cream* and *greenish cream*, the third group *yellowish*, *yellow*, *variegated yellow* and *greenish yellow*, the fourth group *virescent*, *temporary variegated*, *deformed* 1 and *deformed* 2.

As shown in Table 6, *albinotic* has the lowest D/m value of segregation (0,03), while in the other groups there are several mutations showing great divergencies. In the *cream* mutations the D/m values are 8,63, 1,21 and 1,76, in the *yellow* mutations they are 0,67, 1,39, 0,04 and 0,14, and in the *virescens* types 0,41, 1,73, 1,18 and 0,97. KANNA (p. 369) ascribes the great deficiency of recessives in the *light cream* mutation to the low degree of germination, but he does not advance any evidence in support of this opinion.

The previous results thus hold good also here. *A more interesting feature, however, is that every type of mutation has a definite type of segregation.* In 1 of 2 progenies *albinotic* has a deficiency of recessives, *cream* a deficiency in 17 progenies out of 22, *viridis* in 9 progenies out of 12, whereas *yellow* has a deficiency of recessives only in 7 progenies out of 25. The difference between *cream* and *yellow* is statistically

significant ($P < 0{,}01$), and so is the difference between *yellow* and *viridis* ($P < 0{,}01$). This also proves that the *type of mutation* may have an influence on the segregation ratio and on the regular occurrence of an excess or a deficiency of recessives. If the cause is genic, it implies that the type of mutation (though several mutations exist within it) is caused by changes in genes having a similar structure. It may be of interest in this connection to point out that all four *albina* mutations in my tabulation gave low D/m values and all three *xantha* mutations gave high values, though in two cases with a deficiency of recessives and in one case an excess. In HALLQVIST's case, all three *virescens* mutations gave rather high D/m values. In the aggregate, not only on the average, the mutational types in these cases differed from *albina*.

In the following survey only those investigations in DE HAAN's classification (1933) in which another type of mutation in addition to *albina* has been studied are included [1]. In many cases in which the segregation numbers were obtained in field experiments, they must be regarded as unreliable. In several investigations the mutations were used in linkage investigations. In these cases the segregation ratios were calculated from tables of linkage tests. The list does not claim to be complete. Works published later than DE HAAN's have not been included in the list.

Barley. — WIEBE (1924), COLLINS (1927), ROBERTSON (1929). Of the 6 (5) types, *albina* gives a $D/m = 0{,}95$, the *xantha* and *viridis* mutations examined give a $D/m = 1{,}60$. The two P values are 0,20 and 0,08.

Melandrium. — SHULL (1913). Three types were examined, *albina*, *chlorina* and *pallida*. The lowest D/m value was shown by *albina*.

Antirrhinum. — SCHICK and STUBBE (1932). Segregation ratios (from field experiments ?) of 2 *white*, 1 *yellowish white* (called *albina* 530 by the authors) and 7 *light green* mutations (*egrediens* 431, 539, 1565, 1975, 1988, 4203, 4260) are recorded. From one of the *light green* types investigated only 91 individuals were analysed. This mutation — *egrediens* 4203 — has been excluded. In addition to these mutations there appeared a composite chlorophyll mutation, *alma alma*, with an excess of recessives ($D/m = 12{,}5$). The cause of the excess of recessives is not known. 3 of the 6 *egrediens* mutations show also an excess of recessives ($D/m = 1{,}09$, 1,23 and 1,49), the other three, on the contrary, show a deficiency ($D/m = 3{,}86$, 3,88 and 0,98).

Maize. — From the published linkage data it has been possible to obtain figures for 6 *white* mutations, 4 *yellow* mutations, 7 *pale green* mutations and 13 *virescens* mutations. According to DEMEREC (1925), the so-called *xantha* mutation

[1] MORINAGA's investigation of chlorophyll mutations in rice (1932) has been intentionally excluded. The high D/m values, throughout, diminish the reliability of the experiments (field experiments ?). In two F_2 numbers the *albina* mutation gave 38,4 and 19,6 per cent recessives respectively.

TABLE 6. *The Segregation of Different Chlorophyll Mutations.*

Type of Mutation	Segregation	D/m	$\Sigma\chi^2$	P	Author
Oryza sativa					
Albinotic	1105 : 369	0,03	—	—	KANNA, 1935
Light cream	924 : 145	8,68	—	—	»
Heavy cream	4279 : 1374	1,21	—	—	»
Greenish cream	2440 : 756	1,76	—	—	»
Yellowish	399 : 142	0,67	—	—	»
Yellow	4469 : 1552	1,39	—	—	»
Variegated yell.	797 : 265	0,04	—	—	»
Greenish yell.	456 : 154	0,14	—	—	»
Virescent	2223 : 728	0,41	—	—	»
Temporary varieg.	515 : 146	1,73	—	—	»
Deformed 1	118 : 31	1,18	—	—	»
» 2	313 : 93	0,97	—	—	»
Hordeum					
Albina Trebi	616 : 213	0,46	0,212	—	ROBERTSON, 1929
» Cols.	2769 : 882	1,18	1,380	—	»
» » Cr. 59	1936 : 584	2,12	4,468	—	»
»	580 : 194	0,04	0,002	—	WIEBE, 1924
Σ	—	0,95	6,062	0,20	
Xantha	1004 : 375	1,88	3,540	—	ROBERTSON, 1929
Viridis	87 : 21	1,33	1,777	—	COLLINS, 1927
Σ	—	1,60	5,317	0,08	
Melandrium					
Albina	645 : 220	0,29	—	—	SHULL, 1913
Chlorina	206 : 70	0,14	—	—	»
» Back cross	209 : 185	1,21	—	—	»
Pallida	102 : 59	3,42	—	—	»
» Back cross	128 : 150	1,32	—	—	»
Antirrhinum					
Albina 353	214 : 52	2,05	—	—	SCHICK and STUBBE, 1932
» ji	4529 : 1547	0,83	—	—	»
Xantha. Alb. 530	350 : 93	1,95	—	—	»
Viridis, Egrediens					»
» Egr. 431	264 : 100	1,09	—	—	»
» » 539	579 : 213	1,23	—	—	»
» » 1565	369 : 76	3,86	—	—	»
» » 1975	492 : 109	3,88	—	—	»
» » 1988	178 : 73	1,49	—	—	»
» » 4260	110 : 30	0,98	—	—	»
Alma alma	600 : 431	12,46	—	—	»
Zea mays					
White 1	8573 : 2870	0,20	0,040	—	STROMAN, 1924, Tab. 1, LINDSTROM, 1924, Tab. 11
» 2	2325 : 822	1,45	2,105	—	STROMAN, 1924, Tab. 20, 22, LINDSTROM, 1924, Tab. 13
» 3	5216 : 1734	0,10	0,009	—	DEMEREC, 1923, Tab. 30—32, LINDSTROM, 1924, Tab. 8

Type of Mutation	Segregation	D/m	$\Sigma\chi^2$	P	Author
White 5	285 : 91	0,36	0,128	—	DEMEREC, 1923, Tab. 20
» 7	439 : 116	2,23	4,973	—	» » » 21
» 11	993 : 302	1,40	1,948	—	» 1926, » 1, 2
Σ	—	0,96	9,208	0,17	
Yellow 1	1493 : 532	1,32	1,747	—	LINDSTROM, 1918, Tab. 1
» 2	1419 : 474	0,04	0,002	—	» 1925, » 4
» 3	5056 : 1576	2,33	5,407	—	JENKINS and BELL, 1930, p. 256
» 4	3925 : 1231	1,87	3,480	—	JENKINS and BELL, 1930, p. 256
Σ		1,39	10,636	0,03	
Pale green 1	3269 : 1080	0,25	0,064	—	BRUNSON, 1924, Tab. 1
» 2	5148 : 1711	0,10	0,011	—	DEMEREC, 1925, » 3, 13,
» 3	208 : 73	0,38	0,144	—	» » » 19
» 4	7132 : 2219	2,84	8,043	—	» » » 4
Σ		0,89	8,262	0,09	
Xantha	1190 : 431	1,48	2,181	—	TRAJKOVICH, 1924, Tab. 6
Golden 1	2593 : 745	3,58	12,799	—	LINDSTROM, 1918, » 18, 19, 22
» Back cross	337 : 291	1,84	—	—	LINDSTROM, » » 28, 29
Golden 2	1323 : 373	2,86	8,179	—	JENKINS, 1926, p. 487
Virescens 1	851 : 263	1,07	1,151	—	DEMEREC, 1924, Tab. 23
» 2	622 : 203	0,26	0,068	—	PHIPPS, 1929, Tab. 2
» 3	1016 : 373	1,60	2,546	—	DEMEREC, 1924, Tab. 28
» 8	1119 : 362	0,50	0,245	—	» 1926, » 5
» 9	552 : 172	0,78	0,597	—	PHIPPS, 1929, Tab. 5
» 10	1136 : 365	0,61	0,373	—	» » » 6
» 12	2001 : 679	0,40	0,161	—	» » » 7, 40
» 13	1244 : 424	0,39	0,157	—	» » » 8, 50
» 14	341 : 134	1,62	2,611	—	» » » 55, 56
» 15	797 : 302	1,90	3,603	—	» » » 58, 59
» 17	1759 : 536	1,82	3,312	—	» » » 9, 60
» 19	1444 : 473	0,32	0,109	—	» » » 11
» 20	1886 : 619	0,33	0,114	—	» » » 78—81
Σ		0,89	15,047	0,30	
Albina	361 : 130	0,76	—	—	MILES, 1915
Yellowish—white	731 : 260	0,90	—	—	»
Sorghum					
Albina w_1w_1	8116 : 2793	1,45	—	—	KARPER and CONNER, 1931
» w_2w_2	2152 : 699	0,59	—	—	»
Xantha y_1y_1	3899 : 1245	1,32	—	—	»
» y_2y_2	722 : 232	0,49	—	—	»
Virescens v_1v_1	45240 : 12186	20,91	—	—	»
» v_2v_2	10312 : 3162	4,11	—	—	»
Chlorina	689 : 212	1,02	—	—	»
Vicia faba					
Albina	5284 : 1734	0,57	—	—	SIRKS, 1932
Chlorina	3449 : 1019	3,39	—	—	»

found by TRAJKOVICH (1924) is to be referred to the *pale green* class, likewise the *golden* mutation first observed by EMERSON and subsequently closely studied by LINDSTROM (1918).

Undoubtedly the *white* mutations exhibit a rather good segregation ratio with an average D/m of 0,96, while the *yellow*, *pale green* and *virescens* mutations show values of 1,39, 1,91 (0,89) and 0,89 respectively. The P values amount to 0,17, 0,03, $<0{,}01$ (0,09) and 0,30. Thus the *albina* mutations differ significantly from the *yellow* and the *pale green* mutations.

Besides these four main groups of mutations there are in maize quite a number of different types (v. DE HAAN, p. 371). However, they do not form corresponding allel series and are difficult for an outsider to classify. An exhaustive analysis of the chlorophyll segregation in maize — with the aid of the accurate method mentioned on p. 47 — will certainly reveal many problems at present obscure concerning the genetic size of the chlorophyll mutations and the ratio of segregation.

Sorghum. — KARPER and CONNER (1931) give the segregation ratios of 7 mutations, 2 of which are *white*, 2 *yellow*, 2 *virescens* (first white and then green) and 1 *chlorina* (?, DE HAAN, p. 365, calls this type *lutescens*). Here, too, the *albina* mutations undoubtedly give low D/m values. Of the two *virescens* types, one shows a very great deficiency (D/m = 20,91). More than 50,000 individuals were examined. The segregation ratio is 3,71 : 1. According to the authors, this aberration is due to a difficulty in classification. As the family analysis shows no difficulties this explanation seems to me to be rather questionable. The other *virescens* type also shows a great deficiency (D/m = 4,11). In this case the deficiency is thought to be due to the lowered viability of the recessive (p. 300). No reason is advanced for this assumption. About 13,000 individuals were examined. The segregation ratio is 3,26 : 1. Finally, the *chlorina* type also shows a deficiency of recessives, although not to the same extent (D/m = 1,02).

Vicia faba. — In this species SIRKS (1932) has examined a series of multiple allels in *albina* and *chlorina*. The difference in segregation is striking. The D/m for *albina* amounts to 0,57, for *chlorina* to 3,39 (pp. 268 and 271). The great deficiency is considered to be due to a reduced power of germination.

This summarized list shows that in all carefully analysed cases, in barley according to several investigations, in maize, *Sorghum*, rice, *Melandrium*, *Antirrhinum* and *Vicia faba*, the segregation ratios point in the same direction. *Albina mutations are attended by fewer disturbances than xantha and viridis types.* This may be due to the fact that the *xantha* and *viridis* genes, at the same time as the change in the assimilation apparatus, also influence the viability of the seeds. Such a pervading pleiotropic effect is, however, less probable. It is very likely that the *xantha* and the *viridis* genes are of a different structure from those of the *albina* genes, or that these mutations comprise a greater complex of genes, by means of which minor aberrations in the chromosome pairing take place with certain inferior cross-over products as a result.

In conclusion it may be pointed out that the elimination does not

exclusively effect the recessives. In HALLQVIST's material there is an excess of recessives in *virescens* 2 (D/m = 1,3), in my material partially in *xantha* 3 (D/m = 2,0), in *pallida* of *Melandrium* (D/m in F_2 and back cross 3,4 and 1,3 respectively), in *alma alma* of *Antirrhinum* (D/m=12,5), in *white* 2, *yellow* 1, *xantha*, *virescens* 3, 14, 15 of maize (D/m = 1,5, 1,3, 1,5, 1,6, 1,6 and 1,9 respectively). Further, in rice, *yellow* has likewise an excess of recessives (D/m = 1,4). In general, however, the highest D/m values occur in deficiencies of recessives. The investigations carried out by HALLQVIST and me into the question of the lethality of the chlorophyll mutations in barley have shown that the deviations are to a great extent due to gamete elimination. Zygotic lethality occurs along with the gametic lethality in crosses between different chlorophyll mutations, but in the case of *Zwerg* 1, *alboviridis* X 1, X 2, *albina* X 1 and others the great deficiency is entirely due to gamete elimination.

5. SYNTHETIC LETHALITY IN BARLEY AND ITS CAUSES.

Sterility and fertility are intimately associated with each other, and the occurrence of sterility is not exclusively due to cytological aberrations at meiosis. These aberrations indicate only the final stage. The lower limit of sterility has been demonstrated by HALLQVIST (1926). On the basis of aberrations in the segregation ratios and corresponding investigations of germination and the failure to set grain (»Schartigkeit») he succeeded in showing that the deficiency of recessives is in many cases not due to a zygote elimination.

In several of the crosses carried out by NILSSON-EHLE (1922) and HALLQVIST (1926) singular aberrations in the segregation ratios were observed without there being any linkage between the crossed factors. I have calculated the χ^2 value of 26 of these crosses (Table 7). As the mutations crossed together are in a number of instances derived from entirely different lines of barley, the material has been divided into three groups: crosses in which the mutations have quite different origin, crosses in which the mutations have partly the same origin (back crosses in certain cases) and finally crosses in which the mutations are altogether of the same origin. The first group comprises 16 crosses, the second group 8 and the third group 2. The crosses with *Zwerg* 1 are not included in this list.

The first group. — Of the 7 crosses in which the value of P is lower than 0,05, 6 are between *xantha* and *viridis* and 1 between *albina* and *xantha*. Of the 9 crosses where the P value is greater than 0,05 (thus regular segregations), 2 are between *viridis* and *xantha* or *viridis*,

whereas 7 are reciprocal crosses between *albina* or between *albina* and *xantha* or *viridis*. The difference in distribution is statistically significant ($\chi^2 = 6{,}349$). Thus crosses between *xantha* and *viridis* types show greater segregation aberrations than those between *albina* on the one hand and other mutations on the other hand. A very striking feature

TABLE 7. *Crosses between Different Chlorophyll Mutations in Barley.*

Cross	Type of segregation	χ^2	P	Author
Different origin.				
Xantha 1 × *Virescens* 3	9 : 3 : 4	77,544	< 0,01	HALLQVIST, 1926
Xantha 1 × *Virescens* 1	9 : 3 : 4	55,043	< 0,01	»
Xantha 2 × *Virescens* 1	9 : 3 : 4	19,817	< 0,01	»
Albina 3 × *Xantha* 2	9 : 3 : 4	17,304	< 0,01	»
Xantha 1 × *Superchlorina* ...	9 : 3 : 4	10,493	< 0,01	»
Xantha 1 × *Chlorina*	9 : 3 : 4	8,368	0,02	NILSSON-EHLE, 1922
Xantha 2 × *Virescens* 3	9 : 3 : 4	7,183	0,03	HALLQVIST, 1926
Albina 2 × *Xantha* 2	9 : 3 : 4	4,404	> 0,05	NILSSON-EHLE, 1922
Xantha 2 × *Superchlorina* ...	9 : 3 : 3 : 1	4,734	> 0,05	HALLQVIST, 1926
Albina 1 × *Albina* 3	9 : 7	2,355	> 0,05	NILSSON-EHLE, 1922
Albina 4 × *Xantha* 2	9 : 3 : 4	3,898	> 0,05	HALLQVIST, 1926
Albina 2 × *Albina* 3	9 : 7	1,275	> 0,05	NILSSON-EHLE, 1922
Albina 3 × *Xantha* 1	9 : 3 : 4	1,550	> 0,05	HALLQVIST, 1926
Xantha 2 × *Chlorina*	9 : 3 : 3 : 1	2,309	> 0,05	»
Albina 1 × *Albina* 2	9 : 7	0,464	> 0,05	NILSSON-EHLE, 1922
Albina 1 × *Xantha* 2	9 : 3 : 4	0,460	> 0,05	»
Partly identical origin.				
Albina 3 × *Superchlorina* ...	9 : 3 : 4	21,298	< 0,01	HALLQVIST, 1926
Chlorina × *Virescens* 1	9 : 7 (9 : 3 : 4)	7,859	< 0,01	»
Chlorina × *Superchlorina* ...	9 : 3 : 4	7,852	0,02	»
Albina 4 × *Virescens* 1	9 : 3 : 4	7,007	0,03	»
Albina 4 × *Lutescens* 1	9 : 3 : 4	6,010	< 0,05	»
Albina 3 × *Virescens* 1	9 : 3 : 4	2,994	> 0,05	»
Chlorina × *Lutescens* 1	9 : 3 : 3 : 1	3,777	> 0,05	»
Albina 4 × *Virescens* 3	9 : 3 : 4	0,330	> 0,05	»
Identical origin.				
Albina 3 × *Lutescens* 1	9 : 3 : 4	0,714	> 0,05	HALLQVIST, 1926
Superchlorina × *Virescens* 1	9 : 3 : 3 : 1	0,825	> 0,05	»

is that the three crosses showing the highest values of χ^2 (such enormous figures as 77,544, 55,043, 19,817) are *xantha* and *viridis* crosses.

Other groups show uncertain differences. Of crosses between mutations having partly the same origin, two *viridis* crosses have a lower P value than 0,05, one has a higher value (ratio 2 : 1). On the other hand, 3 of the 5 *albina* crosses have a lower value than 0,05 while the other 2 have a higher value (ratio 3 : 2).

Of the 26 crosses cited, (*1*) 3 are between *albina*, (2) 5 between

albina and *xantha*, (*3*) 6 between *albina* and *viridis*, (*4*) none between *xantha* reciprocally, (*5*) 8 between *xantha* and *viridis*, and (*6*) 4 between *viridis* reciprocally. Of the above groups, (*1*), (*2*) and (*5*) are crosses between mutations having quite different origin, (*3*) and (*6*) between mutations having partly or wholly identical origin. The value of $\Sigma\chi^2$ for the 3 *albina* crosses is 4,094 with 3 degrees of freedom ($P = 0{,}2 - 0{,}3$), for the 5 *albina* × *xantha* crosses 27,616 with 10 degrees of freedom ($P < 0{,}01$), and for the 8 *xantha* × *viridis* crosses 185,491 with 18 degrees of freedom (P very much lower than 0,01). The total of χ^2 for *albina* × *viridis* amounts to 38,353 with 12 degrees of freedom ($P < 0{,}01$) and for *viridis* × *viridis* 20,313 with 9 degrees of freedom ($P = 0{,}02$). This method of combination thus shows for certain that crosses in which *xantha* and *viridis* form part more readily produce disturbances than inter-crosses of *albina*. The most interesting features are the increasing values of $\Sigma\chi^2$ in (*1*), (*2*) and (*5*) groups of crosses, viz. 4,094, 27,616 and 185,491.

These groupings undoubtedly furnish an explanation of the synthetic lethality in barley. *Dihybrids more readily produce gamete (and zygote) elimination when xantha and viridis genes meet than in those cases in which albina genes are members.*

As we are faced here with the lowest degrees of sterility, a close analysis is required (see HALLQVIST, 1926, Table 5 and pp. 250—251). In all cases the power of germination is but slightly reduced and the failure to set grain (»die Schartigkeit») but slightly increased in spite of the greatly divergent segregation. The highest rate of sterility is shown by *albina* 3 × *Zwerg* 1. In the dihybrid the percentage of non-germinable caryopses is 3 times greater than that of monohybrid and constantly green plants (6,6 per cent against 2,2 per cent), and the failure to set grain is likewise 3 times more intense (5,2 per cent against 1,7 per cent). In *albina* 4 × *Zwerg* 1, where the segregation is most divergent, the power of germination and the failure to set grain are unchanged. Of the crosses already recorded, *xantha* 1 × *virescens* 3 shows no changes, nor does *albina* 3 × *superchlorina*, whereas *xantha* 1 × *virescens* 1, *xantha* 2 × *virescens* 1 and *albina* 3 × *xantha* 2 show very small changes (in the three cases the percentage of ungerminable caryopses in dihybrid plants in proportion to that in monohybrid and green plants is 1,4, 1,14 and 1,54). The corresponding figures for the failure to set grain are in the first two cases 1,13 and 1,32. In ordinary crossing experiments such a degree of sterility (except in the case of *albina* 3 × *Zwerg* 1?) could hardly have been traced or would have been regarded

as being due to chance. *Albina* 4 × *Zwerg* 1 and *xantha* 1 × *virescens* 3, which furnish the greatest aberrations in their respective groups, do not show the least sign of sterility. In other words, the sterility is so slight that the zygotes are not killed, or but very few of them, and the gametes on the female side do not seemingly become incapable of functioning (with regard to the latter point compare p. 61). It should therefore hardly be too venturesome to ascribe this lethal effect — not to great structural changes in the chromosomes — but to changes in very small pieces of chromosomes or in the genes themselves and disturbances produced by them.

6. SEGREGATION ABERRATIONS IN INDUCED MUTATIONS.

Of the mutations induced in the spring of 1934 there were 25 in F_4 in 1936—1937, and their segregations have been examined. These 25 mutations are distributed as follows: — 14 (15?) in *albina*, 6 (5?) in *xantha*, 2 in *viridis* and 3 in *alboviridis*. One of the 6 *xantha* mutations should possibly be referred to *albina* (D/m = 0,93). It was, it is true, not purely white in colour but was of a dirty white with a faint touch of yellow. In 1935 and in the spring of 1936 it was classified as an *albina* mutation, but to be on the safe side I have now placed it among the *xantha* mutations.

Of the 14 *albina* mutations, 7 have a D/m value ranging between 0 and 1, 2 a D/m value between 1 and 1,5, 3 a D/m value between 1,5 and 2, and 2 a D/m value above 2. The percentages are 50, 14, 21 and *14* respectively. Of the *xantha* mutations, 4 have a D/m value varying between 0 and 1, while the remaining 2 have a D/m value above 2. The percentages are 67 and *33* respectively. Of the 2 *viridis* mutations, 1 has a D/m value of 0,19 and the other a value of 2,32, corresponding to 50 and *50* per cent. Of the 3 *alboviridis* mutations, 1 has a D/m value of 1,50, while the D/m values of the other 2 are above 2,0, equal to 33 and *67* per cent.

If we regard segregation ratios with a D/m value above 2 as diverging for certain from a regular 3 : 1 ratio, the percentages of the various types of mutations will be 14, 33, 50 and 67, that is *albina* mutations are not correlated with segregation aberrations to the same extent as *xantha*, *viridis* and *alboviridis* mutations. The last three types of mutations show an increasing frequency of segregation aberrations. The limit D/m = 2 is only fictitious. In fact even a D/m value equal to 1,5 indicates that the segregation is disturbed or poor.

The frequency of mutations with a D/m value above 1,5 in the various types of mutations is 36, 33, 50 and 100 per cent.

On p. 37 it was shown that the various types of mutations possess a different tendency to produce micromutations. The sequence was as follows: *albina*, (*tiger*), *xantha*, *viridis*, *alboviridis*. The fertility investigations on p. 41 gave the sequence as (*tiger*), *albina*, *viridis*, *alboviridis*, *xantha*. For reasons already given the latter order cannot, however, be regarded as reliable as the former. The former sequence has been confirmed here, although, owing to the smallness of the material, the differences are not significant.

Of these 25 mutations, 24 appeared in both halves of the ears examined. The 25th mutation was produced in field experiments in 2 individuals out of 15. Of the other 24 mutations, 14 were found in the first examination in 1 individual alone, that is, according to the definition given on p. 42, 14, or 56 per cent, of all the 25 mutations could be classified as macromutations. The total number of mutated ears planted in field experiments in this investigation amounted to 47. Of these 47 ears, 22 appeared only in the first mutation analysis and the 22 mutations thus appeared in only one half of the ear. Of these 22 mutations, 17 were found in 1 individual alone, that is 77 per cent.

The 25 induced mutations (the mutation found at the second analysis is counted throughout in this group) occurred in the half-ear first examined in 48 individuals, that is comprising an average of 1,92 individuals. The corresponding figure for the 22 mutations not recovered is 1,50. In the aggregate the 25 mutations showed 106 individuals, that is 4,24 per mutation. At the first analysis, of 283 individuals the ears of these 25 mutations contained 48 mutated individuals, that is 17 per cent. The 22 mutations not recovered later contained 30 mutated individuals out of 191, that is 15 per cent. Altogether the 25 mutations contained 106 mutated individuals out of 616, that is 17 per cent, while the 22 unrecovered mutations contained only 7 per cent (30 out of 437).

It is an important point to establish that of the above-named 25 mutations, 17 having a D/m value below 2,0, in one half-ear appeared in 1,9 mutated individuals, and the remaining 8 mutations having a D/m value of 2,0 and above appeared in 2,0 mutated individuals. Altogether the first group appeared in 4,5 individuals per mutation, the second group in 3,5 individuals per mutation, which indicates the occurrence of a slight difference. In the first 17 mutations the ears consisted of 187 individuals, 32 of which mutated (17 per cent), in the other 8 mutations the ears consisted of 81 individuals, 14 of which mutated (also 17 per cent). Altogether there were 76 mutated individuals (19 per cent) in the first group of 404 individuals, and 28 mutated individuals (14 per cent) in the second group of 195 individuals. Thus there is also here a slight difference.

If the 25 mutations are divided into groups according to declining D/m values, 4 mutations having a D/m value above 3 at the first examination show 49 individuals, 5 of which mutated (10 per cent), totally the figures are 112 and 12 respectively (10,7 per cent). The figures for mutations with a D/m value equal to or higher than 2 are 23,4 and 19,3 per cent ($^{11}/_{47}$ and $^{16}/_{83}$), for mutations with a D/m value between 1,5 and 2,0 the figures are 16,6 and 14,5 per cent ($^{7}/_{42}$ and $^{17}/_{117}$), for mutations with a D/m value between 1,0 and 1,5 they are 14,7 and 14,1 per cent ($^{5}/_{34}$ and $^{11}/_{78}$), for mutations with a D/m value between 0,5 and 1,0 they are 17,2 and 21,9 per cent ($^{5}/_{29}$ and $^{14}/_{64}$), and finally for mutations with a D/m value below 0,5 the figures are 20,8 and 20,6 per cent ($^{15}/_{72}$ and $^{34}/_{165}$). Thus the lowest percentages are shown by the 4 mutations with a D/m value above 3, the highest percentages by the mutations with a D/m value between 2 and 3. This contrast should show that no gradually increasing figures respecting the original range of these mutations occur, in other words all mutations examined here have probably arisen as micromutations irrespective of the segregation ratios.

The result of these segregation analyses (which will be published in detail later) thus indicates that segregation aberrations occur also in the micromutations. *The sequence of the different types of mutations will be as before: albina → xantha → viridis → alboviridis.*

7. CHANGES IN THE TYPES OF MUTATION IN AGEING.

In Table 7 in my paper of 1937 b some figures were given which are of value in this connection. The macromutations, which should have arisen after X ray irradiation, are more intensely selected during ontogenesis as the age of the caryopses increases. In other words, the chromosome disturbances become so intensive as the caryopsis ages that only the smallest changes in the genotype are left (cf. page 43), for the number of mutations consisting of more than one mutated individual increases considerably as the caryopses grow older. At the same time there occur, however, a statistically significant increase in the number of *albina* mutations in the oldest A Series. Besides the selection of macromutations there thus occurs a selection between micromutations of *albina*, on the one hand, and of *xantha* and *viridis*, on the other hand. *Xantha* and *viridis* micromutations are of less selective value than *albina* micromutations. For that reason they disappear earlier than *albina*. The chromosome disturbances in this seed series (1931 A I) are, however, so numerous that even the micromutations of *albina* are associated with such disturbances and on that account occur in a smaller number of individuals per mutation than would otherwise have been the case. (Cf. further p. 84.)

IV. SEGREGATION ABERRATIONS DUE TO GAMETE ELIMINATION.

As already pointed out, HALLQVIST succeeded in demonstrating that the greatly divergent segregation in *Zwerg* 1 was caused by gamete elimination. No zygote lethality or sterility could be traced on the female side. In spite of this, HALLQVIST's inference that only an elimination of male gametes occurs cannot be regarded as proved. At all events it has been proved, however, that the elimination is gametic. [In LINDSTROM's experiments (1918) the mutation *golden* also shows female elimination. The back cross $Gg \times gg$ corresponds to a hypothetical gametic elimination of 13,6 per cent (see below). F_2 (see below) corresponds to the elimination of 10,8 per cent.]

Among the chlorophyll mutations which I have produced by X ray irradiation, six exhibit very great segregation aberrations, all of them with a deficiency of recessives. These mutations are the following: *alboviridis* X 1 and X 2, *albina* X 1 and X 2, and *xantha* X 1 and X 2 (see Table 8).

The segregation ratios of these mutations have been closely studied. *In all cases only elimination of gametes takes place, apparently only on the male side. There is no reduced fertility on the female side, nor is there any reduced vitality of the zygotes.*

Of *alboviridis* X 1, three segregating progenies with D/m values of 10,52, 9,18 and 9,63 respectively have been examined. In two of the progenies the germination of the heterozygotes is somewhat lower than that of the green homozygotes, 97,5 and 91,1 per cent as against 98,9 and 98,1 per cent. In the third progeny, on the other hand, 98,5 per cent of the heterozygotes germinated as compared with 95,8 per cent of the homozygotes. Together the three numbers show 97,7 per cent germinated heterozygous seeds against 97,3 per cent germinated homozygous seeds, that is no decrease in the germination is visible. The total fertility, calculated from the number of seeds per ear, is somewhat lower in the heterozygotes than in the homozygotes, viz. 21,4 against 22,6 seeds per ear. *Alboviridis* X 2 shows the same germination capacity in the heterozygotes as in the homozygotes (98,1 per cent against 98,3 per cent), and the rate of fertility in this mutation is much higher in the heterozygotes than in the homozygotes (48,9 against 44,1 seeds per ear), which can hardly be due to anything but chance. The two mutations having the highest D/m values (16,9 and 7,1), thus exhibit no

TABLE 8. *Number of Seeds/Ear and Germination of Chlorophyll Heterozygotes and their Corresponding Green Homozygotes.*

Type of Mutation	D/m	Fertility		Germination		Number of constant and segregating families
		Heterozygote	Homozygote	Heterozygote	Homozygote	
Alboviridis X 1	10,52	20,5 seeds/ear (945)	23,1 seeds/ear (462)	97,5 % (945)	98,9 % (175)	5 : 10
	9,18	22,7 » (662)	22,1 » (823)	97,1 % (662)	98,1 % (426)	8 : 7
	9,63	22,0 » (616)	22,6 » (474)	98,5 % (616)	95,8 % (407)	7 : 8
Σ	16,94	21,4 » (2223)	22,6 » (1759)	97,7 % (2223)	97,3 % (1008)	20 : 25
Alboviridis X 2	5,21	49,2 » (2068)	49,0 » (196)	97,8 % (2068)	98,0 % (102)	2 : 13
	4,99	48,2 » (915)	43,0 » (774)	98,8 % (915)	98,3 % (416)	7 : 8
Σ	7,11	48,9 » (2983)	44,1 » (970)	98,1 % (2983)	98,3 % (518)	9 : 21
Albina X 1	7,00	25,3 » (809)	24,7 » (667)	95,6 % (809)	97,2 % (356)	8 : 7
Albina X 2	5,15	23,6 » (1394)	21,2 » (403)	94,7 % (1394)	97,3 % (403)	3 : 13
Xantha X 1	2,84	22,3 » (691)	22,7 » (568)	97,8 % (691)	96,5 % (227)	7 : 8
Xantha X 2	2,16	24,1 » (842)	23,6 » (780)	98,1 % (842)	98,0 % (306)	7 : 8
Σ	—	27,8 » (8942)	25,2 » (5147)	97,2 % (8942)	97,5 % (2818)	54 : 82 D/m = 1,58

The parentheses show the total number of seeds.

evidence at all of zygotic lethality nor any reduced fertility on the female side.

Of the four remaining mutations with D/m values of 7,0, 5,2, 2,8 and 2,2, *albina* X 1 and X 2 possibly exhibit a slight zygotic lethality in the heterozygotes, but in return show a considerably larger number of seeds. It may therefore be thought that this higher rate of fertility (i. e. the increase in the number of seeds per ear) tends to weaken the individual seeds and that their germination capacity is thereby reduced. In *xantha* X 1 and X 2 the germination of the heterozygotes is greater than that of the homozygotes and the fertility is about the same in either case.

Totally the heterozygotes show 97,2 per cent and the homozygotes 97,5 per cent germination, that is no difference exists. The fertility is 27,8 and 25,2 seeds per ear respectively, thus very much higher in the heterozygotes than in the homozygotes. This is, however, mainly due to the second progeny of *alboviridis* X 2.

Thus, in the case of another six chlorophyll mutations this investigation has shown that the deficiency of recessives is due to gamete elimination. The statements frequently occurring in the literature with regard to a reduced germination capacity or lethality of the recessive must therefore be regarded as dubious until their correctness has been proved.

The above examinations form the basis of a rather interesting finding. — If the elimination of gametes takes place solely on the male side, it must occur in *alboviridis* X 1 to an extent of approximately 77 per cent. It appears to me to be scarcely probable that not even the slightest trace of a female sterility or zygotic lethality would then occur. Instead it is probable that the lethal process, whereby the male gametes are selected, affects the female gametes too. Since every heterozygous EMC produces two macrospores with the dominant gene and two with the recessive gene, it seems to me to be possible that recessive macrospores are eliminated by the active lethal process and that one dominant macrospore is developed instead. In spite of the elimination of female recessive macrospores no sterility occurs, owing to the fact that the corresponding dominant macrospores may develop.

The question now arises: Is it probable that this possible lethal effect of *the recessive gene* affects the gametes alone and that the zygotes are not affected at all? As mentioned above, the zygotes show no decrease in their capacity of germination. If, for instance, the above-mentioned deficiency of recessives is due to a lower rate of growth in

the pollen tubes of the recessive gametes (cf. HERIBERT NILSSON, 1920), then the germination capacity and especially the rate of germination of the recessive zygotes (HERIBERT NILSSON, 1915, p. 7) should also be reduced. This is not true as regards the germination capacity. In order to ascertain whether it is true in the case of the rate of germination the segregation in a number of lines was determined at the stage when germination has just commenced and the germinal plants had commenced to become visible. As only the white mutations can be distinguished with certainty from the corresponding green zygotes at this early stage, the examination was concentrated on the former.

About a week after this first segregation analysis the numbers analysed showed the ratios of 6980 : 2199 with a D/m value of 2,31, that is a statistically significant deficiency. The first segregation analysis showed the ratio of 4244 : 1328. Thus at this count altogether 60,7 per cent of the material had germinated. The percentage of recessives at the first count was $23{,}83\ \% \pm 0{,}57\ \%$, at the second count $23{,}96\ \% \pm 0{,}45\ \%$. The difference amounts to $0{,}13\ \% \pm 0{,}72\ \%$, that is the mean error is 5 times greater than the difference. *Hence it is fully proved that at least in these lines the deficiency of recessives is not due to decreased viability of the zygote.* As regards rate of germination and germination capacity the recessive zygote is quite as vital as the dominant zygote.

In this connection NILSSON-EHLE's investigations of speltoids and the elimination of gametes in these mutations are of interest. According to NILSSON-EHLE, in the so-called A Series gamete elimination occurs only on the male side. However, the elimination of gametes becomes more intense in proportion as the vitality of the zygotes diminishes. »Auffallend ist somit erstens, dass die Elimination der *a*-Pollenzellen am stärksten ist, wo die Vitalität der Speltoidpflanze am schlechtesten ist . . . Dies ist aber vollkommen verständlich, wenn mit der physiologischen Schwächung des diploiden *aa*-Typus auch eine physiologische Schwächung der männlichen *a*-Gameten Hand in Hand geht.» (1921, p. 29.) The segregation aberration in chlorophyll mutations is not due, as in speltoid mutations, to an impairment of the recessive zygotes, *and probably not to an impairment of the recessive gametes owing to the recessive genes themselves.*

This conclusion is moreover supported by those chlorophyll mutations which produce an excess of recessives, as for instance *alma alma* (*Antirrhinum*). It is scarcely probable that this mutation, which from a certain point of view is sub-lethal, has owing to the change in the chlorophyll factor become more viable in the gametic

stage than the corresponding dominant gamete. This is still more improbable when we consider that the mutation type itself occasionally involves the formation of an excess or a deficiency of recessives (rice, see p. 49).

It has already been shown that the recessive zygote even in those cases where it occurs in greatly deficient numbers does not show any decrease in germination capacity or reduced rate of germination. Careful examinations of the rate of withering of the chlorophyll mutations have shown that this rate is highest in the *light green* and *yellow* mutations, while the *white* and the *mainly white* mutations do not wither so quickly. This applies to both field and laboratory experiments. Naturally, if no water is supplied, the green plants are the first to wither, then the light green and the yellow plants but the white plants still remain erect and rigid. This is undoubtedly associated with differences in anatomical structure. Even in an advanced stage the white mutations have still to a great extent involute leaves, while the light green and the yellow mutations most often show unfolded leaves at an early stage. This probably brings about differences in transpiration in the leaves. *The rate of withering is thus practically speaking independent of the ratio of segregation* and is correlated instead with the occurrence of white areas. No parallelism exists between the segregation ratio and the rate of withering. *Albina* mutations endure for a long time irrespective of the family in which they occur, which is also true of the above-mentioned *alboviridis* mutations, although not to the same extent as the *albina* mutations.

HALLQVIST's inference that only male gametes are eliminated was treated above with a certain reservation. There is a possibility that two of the four macrospores in the heterozygote become non-vital and for that reason one of the two dominant macrospores develops instead. On this hypothesis female sterility occurs only when the *dominant* macrospore also contains a lethal factor or a great chromosomal change. If we assume that the lethality in the recessive gametes occurs in both male and female organs then the segregation ratios show definite laws with respect to the elimination. About 50, 25, 12,5 and 6,25 per cent of the recessive (or of the dominant) gametes are eliminated. In certain cases the percentage of elimination lies between two of these values. However, if a correction is made for disturbances in the segregation ratios due to changes in the physiology of the mother plant the values will again be rather fine.

The following analysis includes only those mutations which have

been recorded in the literature with fairly large numbers. Of mutations with an elimination of 6,25 per cent, only the three mutations having the highest number of examined individuals are included. All mutations recorded in my own experiments and those of other workers showing more than 6,25 per cent elimination, the number of individuals amounting to at least 450, have been included. The 25 per cent class contains the mutation *egrediens* 1565 with 445 individuals, and the 12,5 per cent group the mutation *albina* 530 with 443 individuals. No other material has been excluded from the highest elimination classes.

Of *alboviridis* X 1, one of my induced mutations, 3 progenies with a total segregation ratio of 1970 : 201 and with a D/m value of 16,9 have been examined. The normal gamete formation should have been 0,5 : 0,5, but it was 0,5 : 0,22, that is a hypothetical elimination of 56 per cent took place. The three numbers show an elimination of 53,0, 56,2 and 60,4 per cent (the gamete frequencies are 0,5 : 0,235, 0,5 : 0,219, 0,5 : 0,198). *Alma alma*, which has an excess of recessives, shows a gamete frequency of 0,27 : 0,5, that is an elimination of 45,6 per cent. *Light cream* (rice) shows a gamete frequency of 0,5 : 0,29, that is an elimination of 41,8 per cent. *Albina* X 1 (an induced mutation in barley with the segregation ratio of 664 : 109) gives an elimination of 40,0 per cent. This last value is possibly to be regarded as incorrect, for one family gave a very small deficiency of recessives.

Of *Zwerg* 1 (barley), 27104 individuals have been examined. The segregation is 22204 : 4900, which corresponds to a gamete elimination of 26,0 per cent. In *alboviridis* X 2 (one of my induced mutations) the segregation has been examined in 2 progenies. These two numbers give a total segregation ratio of 2361 : 565, which corresponds to an elimination of 21,8 per cent. One of them gives the ratio of 743 : 161, corresponding to a gamete elimination of 27,0 per cent, and the other one the ratio of 1618 : 404, corresponding to a gamete elimination of 19,2 per cent. This last figure, however, is not correct. Plants with less than 5 ears per plant give the segregation ratio of 1397 : 324, corresponding to a gamete elimination of 23,4 per cent. Plants with more than 5 ears per plant give the segregation ratio of 221 : 80, thus an excess of recessives (corresponding to an elimination of 3,0 per cent!). The differences between the two groups of plants is so great that the value of P is considerably less than 0,01. Thus we find the same state of things here as in *xantha* 3. With a change in the physiology of the mother plant a change also takes place in the segregation ratio. — *Egrediens* 1975 (*Antirrhinum*) gives the segregation ratio of 492 : 109, which corresponds to an elimination of 25,8 per cent, while *egrediens* 1565 shows the segregation ratio of 369 : 76, equivalent to an elimination of 29,6 per cent.

The hypothetical group with an elimination of 12,5 per cent comprises the following mutations: *Virescens* 1 (*Sorghum*), *White* 7, *Golden* 1 and 2 (maize), *xantha* 3 (with more than 5 ears per plant, barley), *xantha* X 1 (one of my induced mutations), *temporary variegated* (rice), *xantha* X 2 (one of my induced mutations), *albina* 530 (*Antirrhinum*) and *xantha* 3 (< 5 ears per plant). *Virescens* 1 gives the segregation ratio of 45240 : 12186 with an elimination of 14,4 per cent. *White* 7 with a segregation of 439 : 166 gives an elimination of 15,8 per cent. *Golden* 1 gives the ratio

of 2593 : 745 with the elimination of 10,6 per cent (in back crosses 337 : 291, equal to an elimination of 13,6 per cent). *Golden* 2 with the segregation ratio of 1323 : 373 gives the elimination rate of 11,7 per cent. *Xantha* 3 (>5 ears per plant) gives the segregation of 606 : 174 with the elimination of 10,6 per cent. *Xantha* X 1 gives the segregation ratio of 539 : 137 with the total elimination of 18,2 per cent. This figure also proves to be incorrect. The material can be divided into two groups, one group comprising plants with less than 5 ears per plant, the other group consisting of plants with more than 5 ears per plant. The segregation ratios are respectively 400 : 108, with an elimination of 14,4 per cent, and 139 : 29, with an elimination of 29,0 per cent. The difference between the two groups in respect to segregation is not significant. Like *xantha* 3, but contrary to *alboviridis* X 2, plant progenies with more than 5 ears per plant show here an increased deficiency of recessives. — *Temporary variegated*, with a segregation ratio of 515 : 146, gives the elimination of 11,4 per cent. *Xantha* X 2, with a segregation of 653 : 173, shows the elimination of 15,8 per cent, a figure which is also probably incorrect. Plants with less than 6 ears per plant give the segregation of 449 : 124, corresponding to an elimination of 13,0 per cent, while plants with more than 5 ears per plant give the segregation ratio of 204 : 49, which corresponds to a 21,4 per cent elimination. *Albina* 530 gives the ratio of 350 : 93 with 15,4 per cent elimination. *Xantha* 3 (with less than 5 ears per plant) with the ratio 329 : 134 gives an elimination of 14,2 per cent.

In the group comprising mutations with 6,25 per cent gamete elimination, only three mutations have been included: *Virescens* 2 (*Sorghum*), *pale green* 4 (maize) and *yellow* 3 (maize). This group, of course, will show incorrect values more readily than any of the other groups. Owing to the low rate of elimination external environmental factors may influence the segregation to such an extent that it loses its regularity. The three mutations having the segregation ratios 10312 : 3162, 7132 : 2219 and 5056 : 1576 give, however, eliminations of 6,0, 5,0 and 5,0 per cent respectively.

Thus the gamete eliminations presented in the above comparison are: in the 50 per cent group, 60,4, 56,2, 53,0, 45,6, 41,8, 40,0, per cent; in the 25 per cent group, 29,6, 27,0, 26,0, 25,8, 23,4, per cent and 29,0, 21,4 per cent; in the 12,5 per cent group, 15,8, 15,4, 14,4, 14,2, 13,0, 11,7, 11,4, 10,6, 13,6, 10,6 per cent, and finally in the 6,25 per cent group, the three included mutations 6,0, 5,0 and 5,0 per cent. It seems to me that these figures demonstrate a definite law as regards the elimination of gametes. The possibility of correcting certain values which lie midway between the postulated ideal values furnishes still further support for this conclusion. An individual treatment of all mutations with more or less divergent values would perhaps also show that these values are adjustable.

If this division of the mutations into classes with definite rates of gamete elimination is justified, it seems to me to be necessary to postulate the occurrence of established processes at meiosis, by means of which the recessive (occasionally the dominant) gametes *in addition to*

the recessive gene are injured in the genome, and this injury kills them or prevents their development.

The synthetic lethality, which HALLQVIST demonstrated in his crosses and which I have previously analysed with respect to the tendency of various mutations to it, furnishes evidence in support of the above view. The most effective synthetic lethality arises in reciprocal crosses between *xantha* and *viridis* mutations *with entirely or partly different origin.* A critical analysis of the segregation ratios will show that the aberrations in these ratios can be explained by assuming gametic elimination in definite proportions.

An analysis has been made of 8 of HALLQVIST's crosses which showed greatly divergent D/m values. Cross No. 22 with a high rate of zygotic lethality has been excluded, likewise Cross No. 56, as no information concerning the gametic or zygotic lethality is given by HALLQVIST. The estimations have been made in such a manner that the elimination has been thought to affect now one gene now the other, and that the lethality in itself has not been considered to become greater because a double-recessive gamete arises. As long as the genes lie in different chromosomes, the two lethal processes, if the lethality is due to irregularities during meiosis (crossing over disturbances, etc.), must of course be independent of each other.

The analysed crosses are the following: —

Zwerg 1 × *albina* 4.
Segregation. 8297 : 1803 : 3161 = 13261

Elimination:
Zwerg 1 = *26,8 %*
albina 4 = 4,6 %

Xantha 1 × *virescens* 1.
Segregation. 3685 : 1191 : 1314 = 6190

Elimination:
Virescens 1 = *14,6 %*
xantha 1 = 2,2 %

Xantha 1 × *virescens* 3.
Segregation. 9091 : 2534 : 3619 = 15244

Elimination:
Xantha 1 = *12,4 %*
virescens 3 = 5,0 %

Xantha 1 × *superchlorina.*
Segregation. 854 : 236 : 321 = 1411

Elimination:
Xantha 1 = *13,0 %*
superchlorina = 8,8 %

Albina 3 × *xantha* 2.
Segregation. 3457 : 1097 : 1345 = 5899

Elimination:
Xantha 2 = 8,6 %
albina 3 = 3,6 %

Xantha 2 × *virescens* 1.
Segregation. 6883 : 2162 : 2781 = 11826

Elimination:
Virescens 1 = 5,8 %
xantha 2 = 4,5 %

Albina 3 × *superchlorina.*
Segregation. 4402 : 1407 : 1716 = 7525

Elimination:
Albina 3 = 8,6 %
superchlorina = 3,1 %

Xantha 2 × *virescens* 3.
Segregation. 4735 : 1491 : 1978 = 8204

Elimination:
Xantha 2 = 4,2 %
virescens 3 = 3,5 %

As the survey shows, the four highest elimination values belong to the hypothetical 25 and 12,5 percentage groups. This tends to enhance the probability that this elimination is not itself due to the recessive genes but to certain processes in the formation of sex cells. It is also probable that the synthetic lethality is not due to the union of recessive factors but to the fact that *chromosomes with definite recessive factors are paired with chromosomes of foreign origin*, thus with a partly different structure. For crosses between mutations with entirely different origin (Table 7), $\Sigma\chi^2$ amounts to 217,201 with 31 degrees of freedom (P greatly below 0,01), for crosses with partly similar origin, 57,127 with 16 degrees of freedom ($P < 0{,}01$), and for crosses with identical origin, 1,539 with 5 degrees of freedom ($P = 0{,}91$).

In some cases the enumerated crosses show a different rate of elimination for the same mutation. There is nothing strange in that. Normally only a few of the mutations employed give a definite gametic elimination. This elimination is therefore increased in crosses with a foreign line. Different lines exhibit unequally great chromosomal changes, and this in turn may explain the unequal elimination.

V. THE MECHANISM OF INDUCED MUTATING.

1. WATER CONTENT, TYPE OF MUTATION AND FREQUENCY OF MUTATIONS.

Natural Differences in Water Content. — In my previous studies I have shown that an increase in the water content of the nucleus also brings about an increase in the frequency of microscopically visible chromosomal aberrations. This increase is entirely (or mostly) due to a diminution in the stability of the chromosomes so that they are more easily fragmented. By means of an examination of series of irradiated seeds with varying water content it should therefore be possible to ascertain the relative frequencies of macro- and micromutations and the change in the types of mutation in this alteration of the nuclear environment.

The frequency of mutations in the following tables has beeen cal-

TABLE 9. *The Frequency of Mutations and Mutants at Different Water Content.*

I. A- and B-Series.

Series	% Mutations	Diff.		% Mutants	Diff.	
1934 A I	$\frac{31}{187} = 16{,}6$			$\frac{56}{4844} = 1{,}15$		
» B I	$\frac{30}{182} = 16{,}5$	+ 0,1 %		$\frac{53}{4675} = 1{,}13$	+ 0,02 %	
1933 A I	$\frac{17}{232} = 7{,}3$		+ 2	$\frac{26}{7295} = 0{,}36$		+ 2
» B I	$\frac{6}{226} = 2{,}6$	+ 4,7 %	− 1	$\frac{9}{6253} = 0{,}14$	+ 0,22 %	− 1
1931 A I	$\frac{17}{141} = 12{,}1$			$\frac{28}{4706} = 0{,}59$		
» B I	$\frac{18}{140} = 12{,}9$	− 0,8 %		$\frac{36}{3691} = 0{,}98$	− 0,39 %	
1934 A IV dry ...	$\frac{12}{195} = 6{,}2$			$\frac{21}{3966} = 0{,}53$		
» B IV » ...	$\frac{7}{115} = 6{,}1$	+ 0,1 %		$\frac{17}{3266} = 0{,}52$	+ 0,01 %	
1934 A IV 1 h ...	$\frac{3}{94} = 3{,}2$		+ 2	$\frac{3}{2160} = 0{,}14$		+ 2
» B IV 1 » ...	$\frac{8}{154} = 5{,}2$	− 2,0 %	− 1	$\frac{15}{3689} = 0{,}41$	− 0,27 %	− 1
1934 A IV 3 h ...	$\frac{7}{106} = 6{,}6$			$\frac{9}{2430} = 0{,}37$		
» B IV 3 » ...	$\frac{3}{146} = 2{,}1$	+ 4,5 %		$\frac{5}{4024} = 0{,}12$	+ 0,25 %	
1931 A IV dry ...	$\frac{6}{89} = 6{,}7$			$\frac{12}{2435} = 0{,}49$		
» B IV » ...	$\frac{1}{71} = 1{,}4$	+ 5,3 %		$\frac{2}{2146} = 0{,}09$	+ 0,40 %	
» A IV 1 h ...	$\frac{4}{78} = 5{,}1$		+ 2	$\frac{10}{2351} = 0{,}43$		+ 3
» B IV 1 » ...	$\frac{5}{78} = 6{,}4$	− 1,3 %	− 1	$\frac{6}{2200} = 0{,}27$	+ 0,16 %	− 0
» A IV 3 h ...	$\frac{7}{103} = 6{,}8$			$\frac{12}{2512} = 0{,}48$		
» B IV 3 » ...	$\frac{4}{82} = 4{,}9$	+ 1,9 %		$\frac{6}{2555} = 0{,}23$	+ 0,25 %	
1935 A VIII	$\frac{4}{92} = 4{,}3$			$\frac{15}{2325} = 0{,}65$		
» B VIII	$\frac{4}{75} = 5{,}3$	− 1,0 %	+ 1	$\frac{10}{1716} = 0{,}58$	+ 0,07 %	+ 2
1932 A VIII	$\frac{4}{50} = 8{,}0$		− 1	$\frac{13}{1379} = 0{,}94$		− 0
» B VIII	$\frac{0}{52} = 0{,}0$	+ 8,0 %		$\frac{0}{1490} = 0{,}00$	+ 0,94 %	
Σ A	$\frac{112}{1367} = 8{,}2$	+ 1,7 %	+ 7	$\frac{205}{36403} = 0{,}56$	+ 0,11 %	+ 9
Σ B	$\frac{86}{1321} = 6{,}5$		− 4	$\frac{159}{35705} = 0{,}45$		− 2

culated from the number of mutations in a plant series. The frequency of mutants, i. e. the number of mutated zygotes in a plant series, is expressed in percentage of the total number of seeds. This has been calculated from the number of individuals per ear in some twenty plant progenies and this number has been multiplied by the known number of ears in the plant series. Corresponding gamete frequencies can be obtained in the usual manner.

Table 9 gives a list of the zygote frequencies in the similarly treated A and B Series. There is a certain probability that the higher value obtained for the A Series ($P = 0{,}03$) is real. Of 11 A Series examined, 9 give higher zygote frequencies than the corresponding B Series. The number of plant progenies containing one or more mutations is also higher in the A Series than in the B Series. Thus seeds showing high frequencies of chromosomal aberrations also give high frequencies of genetic aberrations.

The next table (Table 10: 2 a—c) shows the relative frequencies of the different types of mutations and the frequencies of mutations with one or more mutants. *A striking feature is the high value found for alboviridis in the A Series in contradistinction to the B Series.* In fact χ^2 amounts to 5,484, which corresponds to a P value of 0,02. This high frequency of *alboviridis* mutations is due to the great increase in the 1 mutant class. In the A Series, *alboviridis* with 2 and 3 individuals occurs up to 5,5 per cent, in the B Series up to 3,4 per cent, while *alboviridis* with 1 individual occurs in 20,4 and 9,1 per cent respectively. Probably the high water content brings about an increase in the number of macromutations, which causes the formation of *alboviridis* mutations, in other words these mutations are largely produced by chromosome disturbances. In the case of *tiger*, *xantha* and *viridis* mutations the reverse is generally true. These three types increase the number of their mutations in the dry series (χ^2 amounts to 3,687 with a P value of about 0,05). This increase, however, is due to the decrease in the frequency of *alboviridis*. *Albina* gives an equal number of mutants in both the A and the B Series.

Another tabulation (Table 10: 1 a—c) shows that the percentage of mutations with 1 individual in all types of mutations with the exception of *viridis* is highest in the A class. The high frequency of mutations in seeds with a high water content is therefore probably due to the formation of several macromutations, that is to the increased frequency of chromosomal disturbances.

Water Treated Seed Series. — Since seeds with original differences

TABLE 10. *The Number of Different Mutations within the A- and B-Series.*

		1 a	2 a	1 b	2 b	1 c	2 c	
Type of Mutation	Series	Percentage of Mutations with						Σ
		1 Ind.		2 Ind.		3 Ind.		
Albina	A	$\frac{25}{51} = 49{,}0\ \%$	$\frac{25}{108} = 23{,}1\ \%$	$\frac{13}{51} = 25{,}5\ \%$	$\frac{13}{108} = 12{,}0\ \%$	$\frac{13}{51} = 25{,}5\ \%$	$\frac{13}{108} = 12{,}0\ \%$	$\frac{51}{108} = 47{,}2\ \%$
	B	$\frac{16}{42} = 38{,}1\ \%$	$\frac{16}{88} = 18{,}2\ \%$	$\frac{17}{42} = 40{,}5\ \%$	$\frac{17}{88} = 19{,}3\ \%$	$\frac{9}{42} = 21{,}4\ \%$	$\frac{9}{88} = 10{,}2\ \%$	$\frac{42}{88} = 47{,}7\ \%$
Xantha	A	$\frac{6}{9} = 66{,}7\ \%$	$\frac{6}{108} = 5{,}6\ \%$	$\frac{2}{9} = 22{,}2\ \%$	$\frac{2}{108} = 1{,}9\ \%$	$\frac{1}{9} = 11{,}1\ \%$	$\frac{1}{108} = 0{,}9\ \%$	$\frac{9}{108} = 8{,}3\ \%$
	B	$\frac{6}{11} = 54{,}5\ \%$	$\frac{6}{88} = 6{,}8\ \%$	$\frac{5}{11} = 45{,}5\ \%$	$\frac{5}{88} = 5{,}7\ \%$	—	—	$\frac{11}{88} = 12{,}5\ \%$
Viridis	A	$\frac{8}{15} = 53{,}3\ \%$	$\frac{8}{108} = 7{,}4\ \%$	$\frac{5}{15} = 33{,}3\ \%$	$\frac{5}{108} = 4{,}6\ \%$	$\frac{2}{15} = 13{,}3\ \%$	$\frac{2}{108} = 1{,}8\ \%$	$\frac{15}{108} = 13{,}9\ \%$
	B	$\frac{10}{17} = 58{,}8\ \%$	$\frac{10}{88} = 11{,}3\ \%$	$\frac{6}{17} = 35{,}3\ \%$	$\frac{6}{88} = 6{,}8\ \%$	$\frac{1}{17} = 5{,}9\ \%$	$\frac{1}{88} = 1{,}1\ \%$	$\frac{17}{88} = 19{,}3\ \%$
Alboviridis	A	$\frac{22}{28} = 78{,}6\ \%$	$\frac{22}{108} = 20{,}4\ \%$	$\frac{5}{28} = 17{,}9\ \%$	$\frac{5}{108} = 4{,}6\ \%$	$\frac{1}{28} = 3{,}6\ \%$	$\frac{1}{108} = 0{,}9\ \%$	$\frac{28}{108} = 25{,}9\ \%$
	B	$\frac{8}{11} = 72{,}7\ \%$	$\frac{8}{88} = 9{,}1\ \%$	$\frac{2}{11} = 18{,}2\ \%$	$\frac{2}{88} = 2{,}3\ \%$	$\frac{1}{11} = 9{,}1\ \%$	$\frac{1}{88} = 1{,}1\ \%$	$\frac{11}{88} = 12{,}5\ \%$
Tiger	A	$\frac{5}{5} = 100{,}0\ \%$	$\frac{5}{108} = 4{,}6\ \%$	—	—	—	—	$\frac{5}{108} = 4{,}6\ \%$
	B	$\frac{5}{7} = 71{,}4\ \%$	$\frac{5}{88} = 5{,}7\ \%$	—	—	$\frac{2}{7} = 28{,}6\ \%$	$\frac{2}{88} = 2{,}3\ \%$	$\frac{7}{88} = 8{,}0\ \%$
Σ	A	$\frac{66}{108} = 61{,}1\ \%$	—	$\frac{25}{108} = 23{,}1\ \%$	—	$\frac{17}{108} = 15{,}7\ \%$	—	108
Σ	B	$\frac{45}{88} = 51{,}1\ \%$	—	$\frac{30}{88} = 34{,}1\ \%$	—	$\frac{13}{88} = 14{,}8\ \%$	—	88

TABLE 11. *The Frequency of Mutations and Mutants at Different Water Content.*

II. Water Treated Series.

Series	% Mutations	Diff.		% Mutants	Diff.	
1935 A IV 1 h ...	$\frac{4}{85} = 4{,}7$			$\frac{7}{2443} = 0{,}29$		
» A IV dry ...	$\frac{9}{104} = 8{,}7$	− 4,0 %		$\frac{19}{2998} = 0{,}63$	− 0,34 %	
1934 A IV 1 h ...	$\frac{3}{94} = 3{,}2$		+0	$\frac{3}{2160} = 0{,}14$		+0
» A IV dry ...	$\frac{12}{195} = 6{,}2$	− 3,0 %	−3	$\frac{21}{3966} = 0{,}53$	− 0,39 %	−3
1934 B IV 1 h ...	$\frac{8}{154} = 5{,}2$			$\frac{15}{3689} = 0{,}41$		
» B IV dry ...	$\frac{7}{115} = 6{,}1$	− 0,9 %		$\frac{17}{3266} = 0{,}52$	− 0,11 %	
1931 A IV 1 h ...	$\frac{4}{78} = 5{,}1$			$\frac{10}{2351} = 0{,}43$		
» A IV dry ...	$\frac{6}{89} = 6{,}7$	− 1,6 %	+1	$\frac{12}{2435} = 0{,}49$	− 0,06 %	+1
» B IV 1 h ...	$\frac{5}{78} = 6{,}4$		−1	$\frac{6}{2200} = 0{,}27$		−1
» B IV dry ...	$\frac{1}{71} = 1{,}4$	+ 5,0 %		$\frac{2}{2146} = 0{,}10$	+ 0,17 %	
1934 A VI 3 h ...	$\frac{3}{117} = 2{,}6$			$\frac{6}{3200} = 0{,}19$		
» A VI dry ...	$\frac{1}{135} = 0{,}7$	+ 1,9 %	+1	$\frac{1}{3924} = 0{,}03$	+ 0,16 %	+1
» B VI 3 h ...	$\frac{7}{137} = 5{,}1$		−1	$\frac{15}{4415} = 0{,}34$		−1
» B VI dry ...	$\frac{15}{123} = 12{,}2$	− 7,1 %		$\frac{24}{2900} = 0{,}83$	− 0,49 %	
1931 A VI 3 h ...	$\frac{8}{86} = 9{,}3$			$\frac{16}{2517} = 0{,}64$		
» A VI dry ...	$\frac{6}{81} = 7{,}4$	+ 1,9 %	+1	$\frac{17}{2470} = 0{,}68$	− 0,04 %	+1
» B VI 3 h ...	$\frac{2}{37} = 5{,}4$		−1	$\frac{11}{919} = 1{,}20$		−1
» B VI dry ...	$\frac{6}{52} = 11{,}5$	− 6,1 %		$\frac{14}{1226} = 1{,}14$	+ 0,06 %	
Σ Water Treated	$\frac{44}{866} = 5{,}1$		+3	$\frac{89}{23893} = 0{,}37$		+3
Σ Dry	$\frac{63}{965} = 6{,}5$	− 1,4 %	−6	$\frac{127}{25341} = 0{,}50$	− 0,13 %	−6

in water content give an increased frequency of mutations, it should be expected that treatment with water would increase the frequency still further. The chromosome disturbances in water treated series increase parallelly with the water content (GUSTAFSSON, 1937 a, p. 308). However, this is not the case with the frequency of mutations. The frequency of mutations in my material is certainly lower in water treated seed series than in untreated series.

Table 11 shows that the two frequencies of zygotes are significantly different from each other. In the treated series 89 individuals out of 23893 are mutated, while in the untreated series 127 individuals out of 25341 are mutated. The difference is significant ($\chi^2 = 4{,}643$ with a P value of 0,04). Thus, while the A Series give higher frequencies of mutants than the B Series, the water treated series give lower frequencies than the normal series. The number of plant progenies with mutations is also lower in the water treated series than in the untreated series. The difference between series with an originally high water content on the one hand and water treated series on the other hand will for this reason be still more significant. In the water treated material 6 series show negative differences and 3 series positive differences. The corresponding figures for the A and B Series are 9 series with positive differences and 2 series with negative differences. The differences between the two groups of values is reliable ($\chi^2 = 4{,}848$, $P = 0{,}04$).

Two results in my previous investigations help to classify this singular condition.

In a water treatment of caryopses all nuclei in an embryo do not benefit to an equal extent (GUSTAFSSON, 1936, Table 8). The treatment benefits mainly those nuclei which start mitosis earliest. In proportion as the water treatment increases the number of nuclei near to the starting point of mitosis (the reproduction stage, according to my view) increases. »Die Anzahl Kerne, die Neigung zu Fragmentation zeigen, nimmt also mit der Wasserbehandlung wesentlich zu» (1936, p. 501).

These nuclei, which are close to the starting point of mitosis, are also most easily killed by X ray irradiation. Proximity to the reproduction stage should be the decisive factor (GUSTAFSSON, 1937 b). In that work I demonstrated the probability that the nuclei which first enter mitosis, both after treatment with water and an increased ageing of the caryopses, are the ones most quickly killed. The former circumstance is of value in considering the above results. In the above-mentioned work (Table 1 and p. 29) I showed that the number of

peripheral cells in the intensely moistened series was considerably increased in the starting stages after irradiation. Thus the above genetic results furnish further support for the correctness of this view. The differences between the A and the B Series is due to a *constant* difference between the nuclei (the earliest starting nuclei, however, should also be more numerous in the A Series than in the B Series; cf. GUSTAFSSON, 1937 a). In the water treated series the water content is not uniformly distributed among all nuclei, the supply of water first benefiting those nuclei which start mitosis. At the same time these nuclei are most easily influenced by the irradiation. During the long keeping, to which they have been subjected in these investigations before being sown, a large number of these watery, mutation-rich and at the same time greatly fragment-provided nuclei has become avital and unable to enter into division.

Whilst the A and B Series differ from each other with regard to the number of *alboviridis* mutations this sure positive difference has disappeared in the water treated series (Table 12) and has been replaced by a deficiency instead. The untreated series give 13 per cent *alboviridis*, the water treated series only 5 per cent. *In other words alboviridis mutations arise chiefly in those nuclei which have a high water content and which in consequence give more chromosome aberrations and are more easily killed.* On p. 38 I have for other reasons emphasized that *alboviridis* mutations rather easily arise as macromutations. This view has been corroborated here.

In the A Series the aggregate number of mutations with 1 individual was 61 per cent against 51 per cent in the B Series. In the water treated series the corresponding figures are 45 per cent and 48 per cent respectively (Table 12). The differences are not significant in either group, but the contrary tendency is evident. On p. 76 these differences will be treated still further in respect to the IV and VI Series. The chromosome disturbances are more numerous in the A Series than in the B Series but the macromutations and the *alboviridis* mutations are also more numerous in the former than in the latter. In the water treated series the chromosome disturbances immediately after irradiation are more numerous than in normal series, but in spite of that the frequency of mutations decreases, due chiefly to the diminution in the number of macromutations and especially of *alboviridis* mutations.

The mutual relationship between macromutations and micromutations can thus be made to vary. Drying the seeds before irradiation gives rise to a relatively smaller number of macromutations and a

TABLE 12. *The Number of Different Mutations within the Water Treated Series.*

Type of Mutation	Series	Percentage of Mutations with						Σ
		1 Ind.		2 Ind.		3 Ind.		
Albina	Treated	$\frac{8}{20} = 40{,}0\ \%$	$\frac{8}{42} = 19{,}0\ \%$	$\frac{4}{20} = 20{,}0\ \%$	$\frac{4}{42} = 9{,}5\ \%$	$\frac{8}{20} = 40{,}0\ \%$	$\frac{8}{42} = 19{,}0\ \%$	$\frac{20}{42} = 47{,}6\ \%$
	Dry	$\frac{13}{35} = 37{,}1\ \%$	$\frac{13}{63} = 20{,}6\ \%$	$\frac{12}{35} = 34{,}3\ \%$	$\frac{12}{63} = 19{,}0\ \%$	$\frac{10}{35} = 28{,}6\ \%$	$\frac{10}{63} = 15{,}9\ \%$	$\frac{35}{63} = 55{,}6\ \%$
Xantha	Treated	$\frac{4}{8} = 50{,}0\ \%$	$\frac{4}{42} = 9{,}5\ \%$	$\frac{4}{8} = 50{,}0\ \%$	$\frac{4}{42} = 9{,}5\ \%$	—	—	$\frac{8}{42} = 19{,}0\ \%$
	Dry	$\frac{5}{9} = 55{,}6\ \%$	$\frac{5}{63} = 7{,}9\ \%$	—	—	$\frac{4}{9} = 44{,}4\ \%$	$\frac{4}{63} = 6{,}4\ \%$	$\frac{9}{63} = 14{,}3\ \%$
Viridis	Treated	$\frac{2}{8} = 25{,}0\ \%$	$\frac{2}{42} = 4{,}8\ \%$	$\frac{5}{8} = 62{,}5\ \%$	$\frac{5}{42} = 11{,}9\ \%$	$\frac{1}{8} = 12{,}5\ \%$	$\frac{1}{42} = 2{,}3\ \%$	$\frac{8}{42} = 19{,}0\ \%$
	Dry	$\frac{5}{9} = 55{,}6\ \%$	$\frac{5}{63} = 7{,}9\ \%$	$\frac{4}{9} = 44{,}4\ \%$	$\frac{4}{63} = 6{,}4\ \%$	—	—	$\frac{9}{63} = 14{,}3\ \%$
Alboviridis	Treated	$\frac{2}{2} = 100{,}0\ \%$	$\frac{2}{42} = 4{,}8\ \%$	—	—	—	—	$\frac{2}{42} = 4{,}8\ \%$
	Dry	$\frac{6}{8} = 75{,}0\ \%$	$\frac{6}{63} = 9{,}6\ \%$	$\frac{1}{8} = 12{,}5\ \%$	$\frac{1}{63} = 1{,}6\ \%$	$\frac{1}{8} = 12{,}5\ \%$	$\frac{1}{63} = 1{,}6\ \%$	$\frac{8}{63} = 12{,}7\ \%$
Tiger	Treated	$\frac{3}{4} = 75{,}0\ \%$	$\frac{3}{42} = 7{,}1\ \%$	—	—	$\frac{1}{4} = 25{,}0\ \%$	$\frac{1}{42} = 2{,}3\ \%$	$\frac{4}{42} = 9{,}5\ \%$
	Dry	$\frac{1}{2} = 50{,}0\ \%$	$\frac{1}{63} = 1{,}6\ \%$	—	—	$\frac{1}{2} = 50{,}0\ \%$	$\frac{1}{63} = 1{,}6\ \%$	$\frac{2}{63} = 3{,}2\ \%$
Σ	Treated	$\frac{19}{42} = 45{,}2\ \%$	—	$\frac{13}{42} = 31{,}0\ \%$	—	$\frac{10}{42} = 23{,}8\ \%$	—	42
Σ	Dry	$\frac{30}{63} = 47{,}6\ \%$	—	$\frac{17}{63} = 27{,}0\ \%$	—	$\frac{16}{63} = 25{,}4\ \%$	—	63

larger number of micromutations, water treatment of dry seeds produces on irradiation, theoretically speaking, a greater number of macromutations, but as the nuclei with a high water content are easily killed this increase (which was the case in my experiments) may be counterbalanced by the increased mortality and by keeping the irradiated seeds for a long period a decrease in the number of the macromutations will take place.

2. WATER CONTENT, AGE AND MICROMUTATIONS.

The genetic result of X ray irradiation must be entirely different if the seeds are immediately allowed to germinate and if they are kept for a certain period of time. In the former case the most intense chromosome disturbances are not *automatically* eliminated, instead the disturbed nuclei have time to pass through one or more mitoses before disappearing on account of their inferiority. Long before this the aberrations visible under the microscope (fragments, double constrictions) have disappeared out of the nuclei. After this loss, a number of these nuclei with impoverished genomes continue to exist for some time. Gradually they disappear however, but in view of the fact that not only fragmentation but also the occurrence of unilateral and mutual translocations [1] must in some way be associated with the reproductive stages, many nuclei — even when they have not lost a great part of their gene mass — will be rich in structural changes, which at meiosis cause reduced fertility. If these early nuclei, which in my opinion are close to the reproductive stage, are killed, the genetic result will be that the mutations, which are correlated with chromosome disturbances, structural changes and attendant reduced fertility, will automatically disappear or decrease in number. Of course chromosome aberrations also occur in the nuclei which enter into mitosis last, but they are probably not of such a severe nature. In the preceding chapter it was shown that macromutations, especially of a certain type, disappear if the water treated series are kept for a long period. These mutations are probably caused by structural changes in the chromosomes (segmental interchange, inversion, etc.). Pachytene pairing will therefore be disturbed by the occurrence of non-homologous chromosome parts. — The reverse condition found in the I Series and the later series is explained

[1] The exchange of chromosome segments in *Drosophila* is mostly mutual (MULLER, 1932) and can hardly be explained in another way than by defective reproduction in such non-homologous chromosomes, which lie parallelly close to one another in the resting nuclei.

by this varying period of time in which the seeds were kept after irradiation.

The difference between the A IV and the B IV Series (Table 13) cannot be due to the different behaviour of the very first nuclei, for these nuclei have been killed, but it must be due to the *constant* difference between the nuclei. Since the first, most intensely disturbed nuclei never divide, these series must give more reliable results with respect to the average ratio of the resting nuclei than the I Series.

The number of mutations occurring only in 1 individual is much

TABLE 13. *The Frequency of Mutated Zygotes within the A IV- and B IV-Series.*

	1	2		3	4
Series	Zygotes of Mutations with 1 Ind.	Zygotes of Mutations with > 1 Ind.	Series	Zygotes of Mutations with 1 Ind.	Zygotes of Mutations with > 1 Ind.
1934 A IV dry	$^{9}/_{3966} = 0{,}23$ %	$^{12}/_{3966} = 0{,}30$ %	1931 A IV dry	$^{2}/_{2435} = 0{,}08$ %	$^{10}/_{2435} = 0{,}41$ %
» A IV 1 h	$^{3}/_{2160} = 0{,}14$ %	$^{0}/_{2160} = 0{,}00$ %	» A IV 1 h	$^{2}/_{2351} = 0{,}08$ %	$^{8}/_{2351} = 0{,}34$ %
» A IV 3 h	$^{5}/_{2480} = 0{,}21$ %	$^{4}/_{2480} = 0{,}17$ %	» A IV 3 h	$^{3}/_{2512} = 0{,}12$ %	$^{9}/_{2512} = 0{,}36$ %
Σ A IV	$^{17}/_{8556} = 0{,}19$ %	$^{16}/_{8556} = 0{,}18$ %	Σ A IV	$^{7}/_{7298} = 0{,}10$ %	$^{27}/_{7298} = 0{,}37$ %
1934 B IV dry	$^{2}/_{3266} = 0{,}06$ %	$^{15}/_{3266} = 0{,}46$ %	1931 B IV dry	$^{0}/_{2146} = 0{,}00$ %	$^{2}/_{2146} = 0{,}10$ %
» B IV 1 h	$^{2}/_{3689} = 0{,}05$ %	$^{13}/_{3689} = 0{,}36$ %	» B IV 1 h	$^{4}/_{2200} = 0{,}18$ %	$^{2}/_{2200} = 0{,}09$ %
» B IV 3 h	$^{1}/_{4024} = 0{,}02$ %	$^{4}/_{4024} = 0{,}10$ %	» B IV 3 h	$^{2}/_{2555} = 0{,}08$ %	$^{4}/_{2555} = 0{,}16$ %
Σ B IV	$^{5}/_{10979} = 0{,}05$ %	$^{32}/_{10979} = 0{,}29$ %	Σ B IV	$^{6}/_{6901} = 0{,}09$ %	$^{8}/_{6901} = 0{,}12$ %

greater in the 1934 A IV Series than in the B IV Series (Table 13). While the A Series show 0,19 per cent mutated zygotes, the B Series give only 0,05 per cent. The P value of this difference is much less than 0,01. The number of macromutations thus increases in proportion to the water content. The reverse condition is found in mutations with at least 2 individuals. The B Series give $1\,^{1}/_{2}$ times more mutated zygotes than the A Series. This is due either to the micromutations actually becoming more numerous as the water content of the cells becomes lower or to the fact that the extent of the occurring micromutations in many cases is less, owing to parallelly occurring chromosomal disturbances (cf. the 1931 A I Series). A grouping of the material into mutations with zygotes situated close to each other and with more than 2 mutated zygotes (micromutations in the strict sense of the word) on the one hand, and mutations consisting of 1 and 2 individuals separated from one another (macromutations in a proper sense) on the other hand, will give 18 macromutations and 4 micromutations in

the A Series and 7 macromutations and 10 micromutations (1 uncertain) in the B Series. Thus the difference is more marked.

In the 1931 seed series conditions are different. Here, too, mutations with 1 individual are somewhat more numerous in the A Series than in the B Series (Table 13). As the old seeds in the A Series are doubtlessly in a more abnormal condition (owing to reduced viability, GUSTAFSSON, 1937 b, pp. 22—23), this slight difference is probably due to a much higher rate of mortality among nuclei with macromutations in the A Series than in the B Series. In spite of the abnormal nuclear condition the A Series show a great increase in the number of mutations with at least 2 individuals. The number of zygotes in the A Series is 27 (0,37 per cent) as against 8 in the B Series. The P value of this difference is less than 0,01. In the A Series, the number of real macromutations is 9 and of micromutations 7 (1 uncertain). The corresponding figures for the B Series are 7 and 2 (1 uncertain). The number of micromutations is more than 3 times greater in the A Series than in the B Series. The proportion between the numbers of macromutations in the two serial groups is somewhat higher than that given in Table 13, column 3.

Thus the final results obtained are the following: Micromutations *possibly* arise more readily in dry nuclei than in damp (the 1934 series). In proportion as the seed series grow older the effect of this hypothetical environmental factor is outbalanced by morbid phenomena of old age in the genes. As wet series of old seeds have changed to a greater extent than corresponding dry series the number of micromutations will be higher in the former. Thus in young seed material chromosomal changes and gene changes may *possibly* be the reverse, in aged seed series the two types of mutations run parallelly. Despite this parallelism it is not likely that the gene changes are caused by chromosomal disturbances, although they are attended to a certain extent by such disturbances. If these inferences are correct, the chromosomal disturbances are due to changes in the mechanism of reproduction, while the gene mutations are to a certain extent independent of this mechanism.

Water Treated Series. — First mutations comprising 1 individual. — It has already been shown that the number of macromutations, taken all together, decreased in the water treated series kept for a longer or shorter time after irradiation. This applies, however, only to the 1935—1934 IV and VI Series. The percentage of zygotes of mutations (Table 14, column 5) with 1 individual is here 0,10 and 0,03 respectively

TABLE 14. *The Frequency of Mutations and Mutants within the Water Treated Series.*

	1	2	3	4	5	6
Series	% Mutations	% Mutants	% Macromut.	% Micromut.	% Mutants of Mutations with 1 Ind.	% Mutants of Mutations with > 1 Ind.
1935 A IV dry ...	9/104 = 8,6	19/2998 = 0,63	6/104 = 5,8	3/104 = 2,9	4/2998 = 0,13	15/2988 = 0,50
» A IV 1 h ...	4/85 = 4,7	7/2443 = 0,29	3/85 = 3,5	1/85 = 1,2	3/2443 = 0,12	4/2443 = 0,16
» A IV 3 h ...	10/82 = 12,2	21/1768 = 1,18	5/82 = 6,1	5/82 = 6,1	4/1768 = 0,23	17/1768 = 0,96
1934 A IV dry ...	12/195 = 6,2	21/3966 = 0,53	10/195 = 5,1	2/195 = 1,0	9/3966 = 0,23	12/3966 = 0,30
» A IV 1 h ...	3/94 = 3,2	3/2160 = 0,14	3/94 = 3,2	0/94 = 0,0	3/2160 = 0,14	0/2160 = 0,00
» A IV 3 h ...	7/106 = 6,6	9/2430 = 0,37	5/106 = 4,7	2/106 = 1,9	5/2430 = 0,21	4/2430 = 0,17
1934 B IV dry ...	7/115 = 6,1	17/3266 = 0,52	2/115 = 1,7	5/115 = 4,3	2/3266 = 0,06	15/3266 = 0,46
» B IV 1 h ...	8/154 = 5,2	15/3689 = 0,41	2/154 = 1,3	5/154 = 3,2[1]	2/3689 = 0,06	13/3689 = 0,35
» B IV 3 h ...	3/146 = 2,1	5/4024 = 0,12	3/146 = 2,1	0/146 = 0,0	1/4024 = 0,02	4/4024 = 0,10
Σ 1935, 1934 dry	28/414 = 6,8	57/10230 = 0,56	18/414 = 4,3	10/414 = 2,4	15/10230 = 0,15	42/10230 = 0,41
Σ » » 1 h	15/333 = 4,5	25/8292 = 0,30	8/333 = 2,4	6/333 = 1,8[1]	8/8292 = 0,10	17/8292 = 0,21
Σ » » 3 h	20/334 = 6,0	35/8222 = 0,43	12/334 = 3,9	7/334 = 2,1	10/8222 = 0,12	25/8222 = 0,30
1931 A IV dry ...	6/89 = 6,7	12/2435 = 0,49	2/89 = 2,3	3/89 = 3,4[1]	2/2435 = 0,08	10/2435 = 0,42
» A IV 1 h ...	4/78 = 5,1	10/2351 = 0,43	2/78 = 2,6	2/78 = 2,6	2/2351 = 0,09	8/2351 = 0,34
» A IV 3 h ...	7/103 = 6,8	12/2512 = 0,48	5/103 = 4,8	2/103 = 1,9	3/2512 = 0,12	9/2512 = 0,36
1931 B IV dry ...	1/71 = 1,4	2/2146 = 0,09	1/71 = 1,4	0/71 = 0,0	0/2146 = 0,00	2/2146 = 0,09
» B IV 1 h ...	5/78 = 6,4	6/2200 = 0,27	4/78 = 5,1	1/78 = 1,3	4/2200 = 0,18	2/2200 = 0,09
» B IV 3 h ...	4/82 = 4,9	6/2555 = 0,23	2/82 = 2,4	1/82 = 1,2[1]	2/2555 = 0,08	4/2555 = 0,16
Σ 1931 dry	7/160 = 4,4	14/4581 = 0,31	3/160 = 1,9	3/160 = 1,9[1]	2/4581 = 0,04	12/4581 = 0,26
Σ » 1 h	9/156 = 5,8	16/4551 = 0,35	6/156 = 3,8	3/156 = 1,9	6/4551 = 0,13	10/4551 = 0,22
Σ » 3 h	11/185 = 5,9	18/5067 = 0,36	7/185 = 3,8	3/185 = 1,6[1]	5/5067 = 0,10	13/5067 = 0,26
1934 A VI dry ...	1/135 = 0,7	1/3924 = 0,03	1/135 = 0,7	0/135 = 0,0	1/3924 = 0,03	0/3924 = 0,00
» A VI 3 h ...	3/117 = 2,6	6/3200 = 0,19	1/117 = 0,9	1/117 = 0,9[1]	1/3200 = 0,03	5/3200 = 0,16
1934 B VI dry ...	15/123 = 12,2	24/2900 = 0,83	11/123 = 8,9	3/123 = 2,5[1]	10/2900 = 0,35	14/2900 = 0,48
» B VI 3 h ...	7/137 = 5,1	15/4415 = 0,34	2/137 = 1,5	4/137 = 2,9[1]	1/4415 = 0,02	14/4415 = 0,32
Σ 1934 dry	16/258 = 6,2	25/6824 = 0,37	12/258 = 4,7	3/258 = 1,2[1]	11/6824 = 0,16	14/6824 = 0,21
Σ » 3 h	10/254 = 3,9	21/7615 = 0,28	3/254 = 1,2	5/254 = 2,0[2]	2/7615 = 0,03	19/7615 = 0,25
1931 A VI dry ...	6/81 = 7,4	17/2470 = 0,68	0/81 = 0,0	5/81 = 6,2[1]	0/2470 = 0,00	17/2470 = 0,68
» A VI 3 h ...	8/86 = 9,3	16/2517 = 0,64	5/86 = 5,8	3/86 = 3,5	4/2517 = 0,16	12/2517 = 0,48
1931 B VI dry ...	6/52 = 11,5	14/1226 = 1,14	2/52 = 3,9	4/52 = 7,7	2/1226 = 0,16	12/1226 = 0,99
» B VI 3 h ...	2/37 = 5,4	11/919 = 1,20	0/37 = 0,0	2/37 = 5,4	0/919 = 0,00	11/919 = 1,20
Σ 1931 dry	12/133 = 9,0	31/3696 = 0,84	2/133 = 1,5	9/133 = 6,8[1]	2/3696 = 0,06	29/3696 = 0,78
Σ » 3 h	10/123 = 8,1	27/3436 = 0,79	5/123 = 4,1	5/123 = 4,1	4/3436 = 0,12	23/3436 = 0,68

[1] One mutation not classified.

[2] Two mutations not classified.

as compared with 0,15 and 0,16 in the untreated series, that is together 0,06 as against 0,15 per cent. The P value of this difference amounts to about 0,01.

This does not apply to the 1931 Series. In spite of the long period for which they were kept the moistened series still show an excess of macromutations. In other words, the chromosomal disturbances become so numerous that they even occur in large numbers in nuclei *which are not killed.*

If micromutations are more easily induced in dry than in wet cells of fresh seeds, an excess of such mutations must arise in the untreated series. That is also the case on the average. The untreated 1935, 1934 IV Series show a great excess of zygotes of micromutations (Column 6): 0,41 per cent against 0,21 per cent for the treated. The P value amounts to 0,01. The same thing is shown by the 1931 IV and the 1931 VI Series, whereas the 1934 VI Series give a slight deficiency in the untreated group.

The values of the 1931 series, however, are not unequivocal. As mentioned above, the number of macromutations rises in the moistened caryopses. Therefore, owing to the coincident increase of the still viable chromosomal disturbances, several micromutations may have been transferred to the macromutation group (cf. the 1931 A I Series). In that case the moistened series in the 1931 seeds, like the 1931 A IV Series but contrary to the 1931 B IV Series, in reality show an increase in the frequency of micromutations.

The wet IV Series were treated with water for an unequally long period, some for 1 hour and some for 3 hours. The seeds moistened for 3 hours were afterwards subjected to a more intense X ray irradiation. According to the law of proportion for the ratio of the X ray dosage: the frequency of mutations (TIMOFÉEFF-RESSOVSKY, ZIMMER and DELBRÜCK, 1935), this must bring about a higher frequency of mutations. But if in spite of this both macromutations and micromutations decrease in frequency, as compared with the mutated series, it may be interpreted in such a way that the dry nuclei more readily produce micromutations.

The combined figures show 0,15 per cent zygotes of mutations consisting of 1 individual of the untreated series of the 1935 and 1934 IV seeds against 0,10 and 0,12 per cent for the treated series, and 0,41 per cent zygotes of mutations with at least two individuals as compared with 0,21 and 0,30 per cent for the moistened series. The 1931 untreated series give 0,04 per cent zygotes of mutations with 1 individual against

0,13 and 0,10 per cent for the water treated series. The corresponding figure for zygotes of mutations with at least 2 individuals is 0,26 per cent against 0,22 and 0,26 per cent. Thus, in spite of the treatment by water the frequency of mutations with at least two individuals has not changed even in the old seed series. As treatment by water gives rise to an increase in the number of chromosomal disturbances it is probable, however, that at least some of the micromutations in the 1931 series have, owing to this parallelism, been transferred to the macromutation group.

The tabulation of the frequency of mutations per plant progeny shows 4,3 per cent macromutations in the 1934 and 1935 untreated IV Series as compared with 2,4 and 3,9 per cent in the moistened series. The number of micromutations is 2,4 per cent against 1,8 and 2,1 per cent. In the untreated 1931 IV Series the number of macromutations is 1,9 per cent against 3,8 and 3,8 per cent in the moistened series, while the number of micromutations is 1,9 per cent as compared with 1,9 and 1,6 per cent.

This last comparison furnishes support to the view that micromutations arise more readily in dry nuclei of fresh seeds than in nuclei with a high water content. If this conclusion is correct, it is therefore evident that although micromutations may be attended by chromosomal aberrations they are not caused by such aberrations.

3. AGE AND FREQUENCY OF MUTATIONS.

The continuous change which the chromosomes undergo in ageing leads to an accumulation of disturbances in the nucleus so that finally the nucleus loses its capacity of entering into division. However, those nuclei which have not aged quite so much can start a mitosis, but owing to disturbances in the reproductive mechanism chromosome fragments and fusions arise (NAVASHIN and GERASSIMOVA, 1935), similar to those which are formed after X ray irradiation. Hence the genetic disturbances, which arise owing to ageing (STUBBE, 1935; CARTLEDGE and BLAKESLEE, 1934), are to a great extent associated with or possibly due to chromosomal disturbances. Is it possible then for changes in the genes to arise simultaneously with but independently of the age phenomena in the chromosomes? This important question (to which an affirmative answer was given in the foregoing pages) has so far not been cleared up, although cytological investigations of *Datura* have demonstrated that the so-called gene mutations in aged seeds are not attended by cytologically visible disturbances.

Let us first consider the total frequency of mutations in the VI Series (Tables 14 and 15). In the four parallel series, the 1934 series shows 0,7, 2,6, 12,2 and 5,1 per cent mutations against 7,4, 9,3, 11,5 and 5,4 per cent for the 1931 series, and together 5,1 per cent against 8,6 per cent. The zygote frequencies are 0,03, 0,19, 0,83 and 0,34 per cent as compared with 0,68, 0,64, 1,14 and 1,20 per cent, together 0,32 per cent against 0,81 per cent. Thus the frequency of mutations has not increased to the same extent as the frequency of mutants.

Macromutations in the strict sense show frequencies of 0,7, 0,9, 8,9 and 1,5 per cent against 0,0, 5,8, 3,9 and 0,0 per cent. The 1934 series

TABLE 15. *Mutation Frequency in Aged Seeds.*

Series	% Mutations	% Mutants	% Mutants of Mutations with 1 Indiv.	% Mutants of Mutations with > 1 Indiv.
Σ 1934 A VI, B VI	$^{26}/_{512} = 5{,}1$	$^{46}/_{14489} = 0{,}32$	$^{13}/_{14489} = 0{,}09$	$^{33}/_{14489} = 0{,}23$
Σ 1931 A VI, B VI	$^{22}/_{256} = 8{,}6$	$^{58}/_{7182} = 0{,}81$	$^{6}/_{7182} = 0{,}08$	$^{52}/_{7182} = 0{,}73$
1934 B III dry.....	$^{3}/_{80} = 3{,}8$	$^{4}/_{1983} = 0{,}20$	$^{2}/_{1983} = 0{,}10$	$^{2}/_{1983} = 0{,}10$
1933 » »	$^{14}/_{115} = 12{,}2$	$^{30}/_{2874} = 1{,}26$	$^{7}/_{2874} = 0{,}30$	$^{23}/_{2874} = 0{,}96$
1932 » »	$^{11}/_{68} = 16{,}2$	$^{23}/_{1422} = 1{,}62$	$^{7}/_{1422} = 0{,}49$	$^{16}/_{1422} = 1{,}13$
1934 B III 1 1/2 h.	$^{7}/_{93} = 7{,}5$	$^{19}/_{2105} = 0{,}90$	$^{1}/_{2105} = 0{,}05$	$^{18}/_{2105} = 0{,}86$
1933 » »	$^{5}/_{120} = 4{,}2$	$^{11}/_{2428} = 0{,}46$	$^{1}/_{2428} = 0{,}04$	$^{10}/_{2428} = 0{,}42$
1932 » »	$^{11}/_{88} = 12{,}5$	$^{20}/_{2422} = 0{,}83$	$^{5}/_{2422} = 0{,}21$	$^{15}/_{2422} = 0{,}62$
1931 » »	$^{6}/_{32} = 18{,}8$	$^{11}/_{1049} = 1{,}05$	$^{3}/_{1049} = 0{,}29$	$^{8}/_{1049} = 0{,}76$
1934 B III 3 1/4 h.	$^{1}/_{105} = 0{,}95$	$^{4}/_{2618} = 0{,}15$	$^{0}/_{2618} = 0{,}00$	$^{4}/_{2618} = 0{,}15$
1933 » »	$^{5}/_{101} = 5{,}0$	$^{12}/_{2688} = 0{,}45$	$^{2}/_{2688} = 0{,}07$	$^{10}/_{2688} = 0{,}37$
1932 » »	$^{3}/_{136} = 2{,}2$	$^{13}/_{4068} = 0{,}32$	$^{2}/_{4068} = 0{,}05$	$^{11}/_{4068} = 0{,}27$
1931 » »	$^{1}/_{49} = 2{,}0$	$^{1}/_{1050} = 0{,}10$	$^{1}/_{1050} = 0{,}10$	$^{0}/_{1050} = 0{,}00$

together show 2,9 per cent against 2,7 per cent for the 1931 series. Zygotes of mutations with 1 individual occur in 0,03, 0,03, 0,35 and 0,02 per cent in the 1934 series, and in 0,00, 0,16, 0,16 and 0,00 per cent in the 1931 series, that is together in 0,09 per cent against 0,08 per cent. We thus obtain the following result: *In spite of the great change in the chromosomes with the ageing of the seeds fewer genetically discernible chromosomal aberrations (macromutations) appear.* In other words, the chromosomal aberrations become so potent that they are eliminated to a greater extent during ontogenesis than in fresh caryopses.

The zygote frequencies of mutations appearing in at least 2 individuals are 0,00, 0,16, 0,48 and 0,32 per cent in the 1934 series as compared with 0,68, 0,48, 0,99 and 1,20 per cent in the 1931 series, together 0,23 per cent against 0,73 per cent. The number of micromutations per

plant progeny also increases with age. In the 1934 series this frequency of mutations is respectively 0,0, 0,9, 2,5 and 2,9 per cent as compared with 6,2, 3,5, 7,7 and 5,4 per cent in the 1931 series; together 1,6 per cent against 5,5 per cent. In ageing the micromutations increase in number relatively as well as absolutely. Thus their occurrence is probably not due to the intensity of the chromosomal disturbances but is an autonomic phenomenon caused by age phenomena in the genes themselves. Of course micromutations may be, and certainly are, frequently attended by structural changes in the genome without for all that being caused by these changes.

The VI Series are particularly reliable for an investigation like the above, as they were not subjected to such an intensive irradiation as the other series. The figures for the so-called B III Series also show considerably less regularity, at any rate that applies to the $3\,^1/_4$ h. moistened caryopses. In the dry series and partly in the $1\,^1/_2$ h. series there is a definite parallelism between age and frequency of mutations. As these seeds were kept for 8 months before being sown, while the VI Series were kept for only 2 months, this difference may perhaps be the cause of the partly different behaviour.

The frequency of mutations in the B III dry series rises in the seeds of the three crops examined from 3,8 above 12,2 to 16,2 per cent (Table 15). The frequency of zygotes increases simultaneously from 0,20 above 1,26 to 1,62 per cent. Mutations with 1 individual occur in the seeds of the three different years in 2,5, 6,1 and 10,3 per cent. The corresponding zygote frequencies are 0,10, 0,30 and 0,49 per cent. The number of mutations comprising at least 2 individuals amounts to 1,3, 6,1 and 5,9 respectively, i. e. the number increases somewhat more rapidly than the number of mutations with 1 individual. The frequency of zygotes in mutations with at least 2 individuals shows a still greater increase: from 0,10 above 0,96 to 1,13 per cent. Thus an increase in the number of micromutations is indisputable. Simultaneously with the ageing of the seeds chromosomal as well as gene disturbances are induced but they are probably independent of each other.

In the $1\,^1/_2$ h. moistened series there is a certain parallelism in the different columns. The value of the frequency of mutations, mutations with more than 2 individuals, frequency of zygotes and zygote frequency of mutations with at least 2 individuals are, however, too high in the 1934 series.

The $3\,^1/_4$ h. moistened caryopses show no such regularity other than the parallelism between age and frequency of macromutations.

It is a difficult matter to decide as to whether this want of agreement with the other series is due to mere chance.

In my previous paper (1937 a, Table 20) I demonstrated the *gradual* change in the chromosomes with their ageing. The frequency of mutations likewise increases progressively. In *Datura*, CARTLEDGE and BLAKESLEE also observed a steady rise in the frequency of mutations. In the material of the three oldest years the frequency of mutations was 8,1 per cent, in the material of the three intermediate years it was 3,8 per cent and in the three youngest years 1,2 per cent.

Thus the frequency of mutations rises in their material with the ageing but it rises also with the decrease in the viability of the seed material employed. The two authors mentioned above deny such a correlation (p. 107). Seeds which showed a germination rate of 0—30 per cent gave, however, a mutation frequency of 6,4 per cent, seeds with a germination rate of 30—60 per cent gave a frequency of 4,4 per cent, seeds with a germination rate of 60—80 per cent gave a frequency of 3,7 per cent and, finally, seeds with a germination rate of 80—100 per cent a frequency of 2,7 per cent. The parallelism is obvious. Selective mutability, which HERIBERT NILSSON (1931) conceived to be the explanation of the origin of mutations from X ray irradiated or aged material, is nevertheless not present. The frequency of mutations rises with ageing, owing to age phenomena in the genes and the chromosomes, but at the same time the viability decreases. (Evidence in support of this view is produced in my paper 1937 b.)

4. AGE AND TYPE OF MUTATION.

In the first part of this paper I endeavoured to show that *albina* mutations, on an average, involve smaller changes in the genotype than other types of chlorophyll mutations. These latter types — with the exception of the *tiger* types — are to a great extent correlated with minor disturbances at meiosis, some of them (*alboviridis*) are, moreover, frequently caused by chromosomal disturbances. In crosses between different spontaneous chlorophyll mutations inter-crosses and reciprocal crosses between *xantha* and *viridis* produced great disturbances in the segregation ratios.

In ageing a good many chromosomal aberrations are induced, probably owing to the degeneration of the reproductive mechanism. Now if *xantha* and *viridis* mutations involve such a great change in the genotype that they themselves cause sterility or gametic lethality, they

must also to a greater extent than *albina* mutations be subjected to the disturbances which arise with ageing. For that reason they do not possess the selective value of the *albina* mutations. In an earlier work (1937 b) I have shown that *albina* mutations are the commonest type of mutation in the oldest series of seeds with a high water content (the 1931 A I Series). The explanation of this was that cells with induced *xantha* and *viridis* mutations, owing to their characteristic changes in

TABLE 16. *Age and Type of Mutation.*

Series	White Mutations with		Σ	Non-white Mutations with		Σ
	1 Ind./ear	> 1 Ind./ear		1 Ind./ear	> 1 Ind./ear	
1934 A VI dry ...	—	—	0 %	1	—	100 %
1931 » » ...	—	3	50 %	—	3	50 %
1934 A VI 3 h. ...	1	—	33 %	—	2	67 %
1931 » » ...	2	3	63 %	2	1	37 %
1934 B VI dry ...	5	2	47 %	5	3	53 %
1931 » » ...	2	3	83 %	—	1	17 %
1934 B VI 3 h. ...	1	2	43 %	—	4	57 %
1931 » » ...	—	1	50 %	—	1	50 %
Σ 1934	7	4	42 %	6	9	58 %
Σ 1931	4	10	64 %	2	6	36 %
1934 B III dry ...	1	—	33 %	1	1	67 %
1933 » » ...	3	2	36 %	4	5	64 %
1932 » » ...	5	2	64 %	2	2	36 %
1934 B III 1 1/2 h.	—	3	43 %	1	3	57 %
1933 » »	—	1	20 %	1	3	80 %
1932 » »	3	3	55 %	2	3	45 %
1931 » »	1	1	33 %	2	2	67 %
1934 B III 3 1/4 h.	—	—	0 %	—	1	100 %
1933 » »	—	3	60 %	2	—	40 %
1932 » »	1	1	67 %	1	—	33 %
1931 » »	1	—	100 %	—	—	0 %
Σ 1934, 1933.....	4	9	37 %	9	13	63 %
Σ 1932, 1931.....	11	7	56 %	7	7	44 %

the genotype, quickly disappeared in the course of ontogenesis. What are the facts with respect to the series examined here? (Table 16.)

The four 1934 VI Series gave 26 mutations, 13 of which consisted of mutations in 1 individual, 13 of mutations comprising at least 2 individuals. Of the former, 7 are *albina* mutations, 6 of another nature while of the latter, 4 are *albina* and 9 of another nature. Thus the *albina* mutations amount to 54 per cent in the first group and 31 per cent in the second group. The 1931 series gave 22 mutations: 6 mut-

ations in 1 individual and 16 in at least 2 individuals. In the first group 4, or 67 per cent, are *albina*, in the second group, 10, or 63 per cent. The differences between the 1934 and the 1931 series are not statistically significant but the tendency is that postulated.

In the 1934 and 1933 B III dry Series there appear altogether 17 mutations. The percentage of *albina* in the group of mutations with 1 individual amounts to 44, in the group with at least 2 individuals to 25. The corresponding figures for the 1932 dry series are 71 and 50 per cent. The number of *albina* mutations has increased in both groups. Moreover, two *non-white* mutations in the 1932 series belong to the *tiger* type, which as shown on p. 38 gives micromutations to relatively the same extent as *albina*.

In the 1934 and 1933 $1\,^1/_2$ h. Series the percentage of *white* mutations in the two groups is 0 and 40 respectively, while the corresponding figures for the 1932 and 1931 series are 50 and 44 per cent. Thus there is also here an evident increase.

Finally, in the 1934 and 1933 $3\,^1/_4$ h. series the percentages of *albina* mutations are 0 and 75, in the 1932 and 1931 series, on the other hand, the percentages are 67 and 100. Thus in spite of divergencies in other respects these series show the same state of things.

These results undoubtedly prove that the frequency of the *albina* mutations increases considerably with age, while the other types of mutations disappear. The course of selection is probably as follows: With the increased chromosomal disturbances *xantha* and *viridis* macromutations disappear first, and afterwards *albina* macromutations. Owing to their being easily disturbed cytologically, *xantha* and *viridis* micromutations are subsequently transferred to the macromutation group. Not until after that does this happen to *albina* micromutations. *Hence the types of mutations as a whole have different selective values.*

VI. THE DIFFERENT GENETIC SIZE OF THE CHLOROPHYLL MUTATIONS.

The starting-point of the following discussion is the finding that a certain group of induced chlorophyll mutations (*alboviridis*) arise more readily in cells in which intense chromosomal disturbances have been produced, and that I have succeeded on the basis of this fact to establish a genetic proof of the differential sensitivity of the resting nuclei. From this it may be concluded that the *alboviridis* mutations,

on an average, are not due to changes in solitary genes but to cytological changes in the chromosomes, that is to an interaction between several genes.

Now as transitions from macromutations to micromutations are also found in the *alboviridis* group, the chromosome segments, which have been changed by irradiation and which give rise to the mutation, either become smaller in size or the lethal effect disappears for some reason or other. If the former explanation is correct, the micromutations with the widest range of individuals per mutated ear can no longer be characterised as chromosome mutations. The only *alboviridis* mutation spontaneously arisen in Gullkorn (*alboxantha*, NILSSON-EHLE) does not imply a change in a large chromosome segment but is probably a change in one or a few genes.

If the *alboviridis* mutations are on the average correlated with great structural changes in the chromosomes they can hardly be due to anything but deficiencies (deletions). It is then remarkable that none of the induced *alboviridis* mutations manifest a reduced capacity of germination or a lowered fertility in the heterozygote. The former circumstance argues in a certain measure against the deficiency idea. As pointed out by DEMEREC (1935 b), the deficiency mutations in *Drosophila* are associated with severe lethal effects. Since barley, like *Drosophila*, is to be regarded as an originally diploid organism (possibly contrary to maize), the lethal effect of deficiencies should be about the same in barley as in *Drosophila* and the most powerful deletion mutations in particular (*alboviridis*) should in some respect exhibit this lethal effect.

An important fact is that the cases of gametic elimination previously discussed can be grouped into classes with a postulated occurrence of 50, 25, 12,5 and 6,25 per cent elimination of recessive gametes. *In the highest elimination class, however, only induced mutations occur, in the second highest elimination class, Zwerg 1 is the only spontaneous mutation.* Thus by means of irradiation new types of mutations are produced, which are very seldom produced spontaneously. This is undoubtedly a proof of the destructive genetic effect of X ray irradiation. Still it is remarkable that no sterility in the heterozygotes nor any reduced capacity of germination has ever been found in these cases. We must therefore assume either that in spite of this the deficiencies, which produce *alboviridis* mutations and which involve large parts of chromosomes, have no lethal effect or that the chromosomal changes

are so slight that for that reason they do not cause any decrease of vitality even in a homozygotic stage (cf. above).

The situation is still more complicated in the case of the *xantha* and *viridis* mutations. While the *alboviridis* mutations occur in cells, which are easily killed and which have a large number of disturbances, and are therefore most frequently macromutations, there are in these two types of mutations numerous transitions from macromutations to micromutations, from mutations conditioned by changes of the chromosome structure to mutations that cannot be distinguished from gene mutations. But among the micromutations there also exist transitions from mutations with good segregation ratios to those with poor segregation ratios. Nevertheless the *xantha* and *viridis* mutations exhibit a greater tendency than the *albina* mutations to be associated with segregation aberrations and with the occurrence of macromutations. According to the deletion interpretation, they should therefore be due to changes in larger parts of chromosomes than the *albina* mutations. No lethal effect exists, however, in the zygotic stage. The fertility of the heterozygote and the capacity of germination of the recessive are not reduced. Thus we find the same contrast here as in the *alboviridis* mutations.

Finally we come to the *albina* mutations. In an investigation of the rate of germination in families with a large deficiency of recessives (p. 62) I was able to show that this rate was not lower in the recessive than in the heterozygote and the dominant homozygote. Nor was there any decrease in fertility and capacity of germination in those mutations which showed great segregation aberrations.

The following general conclusion may thus be drawn: *The varying tendency of the mutational types to produce macromutations and mutations with great segregation aberrations must be due either to a difference in the structure of the genes or to a jointly mutating of unequally large blocks of genes.*

The unequal selective capacity of the mutational types indicates that chromosome disturbances on a larger scale bring about an elimination of those cells, where *alboviridis*, *viridis* and *xantha* mutations than where *albina* mutations occur. The first three types of mutations in themselves involve relatively great changes in the genotype. This brings about a reduction of the selective value.

The synthetic lethality in barley shows that such a lethality occurs more readily when *xantha* and *viridis* mutations are inter-crossed or crossed with some other type of mutation. At the same time the differences will be greatest in crosses between mutations of entirely different

origin. The lethality must therefore be connected in some way or other with disturbances at or after the chromosome pairing. According to the previous argument this implies that either *xantha* and *viridis* genes have a larger corpuscle size or that these mutations are associated with a loss not of single genes but of blocks of genes. The changes in the structure of the chromosomes involve difficulties in effecting a regular chromosome pairing, and the irregular chromosome pairing brings about the occurrence of crossing-over products, which reduce the viability of the recessive gametes so that they are eliminated in definite frequencies. The lowest limit of the sterility phenomenon is when individual genes have disappeared or changed position. The disturbances have an increasingly greater effect in proportion as the size of the gene corpuscles increases or as the blocks of genes change position or are lost. The mutations which give an excess of recessives in the segregation analyses show that the recessive gene does not by itself cause an elimination of gametes.

In this connection an investigation by TIMOFÉEFF-RESSOVSKY, ZIMMER and DELBRÜCK (1935) is well worth mentioning. These investigators were able to show that the two genes *W* and bb_l^x possess a very unequal spontaneous capacity of mutation. *White* mutates to its recessive allel *w* only once in 300000, while bb^{lx} spontaneously mutates to *Bb* once in 12000. If the genes are subjected to a certain X ray dosage the corresponding frequencies of mutations are 1 : 2500 and 1 : 1800, that is the genes are now about equally labile. The spontaneous difference in stability is inevitable, as also is the difference in stability eliminated after X ray irradiation. *Differences in stability* (or the elimination of differences in stability, as in the above instance) *may, however, arise quite simply owing to the fact that the irradiated genes vary in size.* If the more stable gene has a greater »molecular volume», it should, when exposed to the action of the X ray irradiation, be more easily changed, because it is struck by the bombarding electrons to a greater extent than smaller genes. The *white* gene in *Drosophila melanogaster* is known for its capacity of forming multiple allels. *It appears to me to be probable that genes with large corpuscles should produce allel series more easily than small genes.*

DEMEREC (1935 b) and TIMOFÉEFF-RESSOVSKY, ZIMMER and DELBRÜCK (1935) have endeavoured to show that a gene is equivalent in size to a single molecule — not consisting of a molecular aggregate. The evidence they advance in support of this inference (DEMEREC, p. 128, and TIMOFÉEFF-RESSOVSKY, ZIMMER and DELBRÜCK, p. 238)

does not seem to me, however, to be conclusive. The above division of the chlorophyll mutations into different groups with a parallelism between phenotypic properties and segregation aberrations is of great interest from a phylogenetic point of view. The different groups of dominant chlorophyll allels must differ from one another, the genes either possess corpuscles of unequal size or to a more or less degree be adherent to other genes. If the various chlorophyll genes are of a phylogenetically different origin and structure, they may, provided they consisted not of single molecules but of groups of molecules, have changed in such a manner that the larger molecular groups (*xantha* and *viridis*) have in the course of time mutated (split up?) so that they have to some extent had time to become equivalent to genes having fewer molecules or a smaller molecular size (*albina*).

However that may be, the present investigation has shown that different types of genes for the formation of chlorophyll are genetically dissimilar. Probably they possess a different structure, either consisting of a different corpuscle size or of an unequally strong attraction to neighbouring genes. If the latter explanation is the correct one, in certain types of mutations blocks of genes, not single genes, always or very often mutate together.

SUMMARY.

The paper reports further results from the investigation of X raying barley seeds, some cytological results of which have been published in GUSTAFSSON, 1936 and 1937 a and b.

1. About 600 chlorophyll mutations have been produced by X raying. Most of them belong to five phenotypical groups: *albina*, *xantha*, *viridis*, *tiger* and *alboviridis*.

2. In the progenies of X rayed seeds, *albina* (and *tiger*) mutations have a definite tendency to contain more mutated individuals per mutation than *xantha*, *viridis* and *alboviridis*. The cause of this fact is probably that the *albina* mutations involve smaller changes of the genotype than the other mutations. The hypothetical sequence in the genotypical size of the different mutation types is: (*albina* → *tiger*) → *xantha* → (*viridis* → *alboviridis*).

3. Mutations, arisen in one mutated individual per mutation, are probably associated with great structural alterations within the genome (macromutations). The ears, in which these macromutations have arisen, show a rather marked sterility. This sterility is most pronounced

in the cases of *xantha*, *viridis* and *alboviridis* mutations. — The micromutations, consisting of 2—3 or more mutated individuals per mutation, show no connection with such a sterility. Thus the micromutations probably consist of changes in single genes or in small gene blocks.

4. The segregation ratios of 25 induced chlorophyll mutations in the fourth generation after irradiation were examined. Several of the induced mutations show great deficiencies of recessives. The tendency to be connected with such aberrations in segregation is most pronounced in the cases of *viridis* and *alboviridis* mutations.

5. In barley, as well as in a series of other plants species, spontaneous *xantha* and *viridis* mutations are often connected with great segregation aberrations. The segregation ratios of *xantha* mutations in barley, in particular, show great variations with alterations in the internal physiological characters of the mother plant.

6. In rice (KANNA, 1935), the *type of mutation* has an influence on the segregation ratios and on the regular occurrence of an excess or a deficiency of recessives.

7. The synthetic lethality in barley (HALLQVIST, 1926) is explained by the fact that dihybrids more readily produce gamete and zygote eliminations when *xantha* and *viridis* genes meet than in those cases in which *albina* genes are members, i. e. *xantha* and *viridis* genes have a different structure from the *albina* genes or are — as postulated above — associated with greater changes of the genotype.

8. Six examined chlorophyll mutations in barley with great segregation aberrations show no sign of a zygotic elimination. No decrease in germination capacity and fertility of the heterozygotes in comparison to the green homozygotes can be traced, nor is any decreased germination rate or viability of the recessive found. Thus only gamete elimination, probably in definite elimination frequencies, occurs.

9. The types of mutation in different cell environments have been recorded. In the so-called A and B Series with an original difference in water content, the A Series show the highest frequencies of mutations and mutated zygotes. These high mutation and mutant rates are caused by an excess of macromutations, especially macromutations of *alboviridis*. As the A Series show more pronounced chromosome disturbances than the B Series (GUSTAFSSON, 1937 a), the above-mentioned fact may be explained in such a manner that macromutations, especially macromutations of *alboviridis*, are caused or at least attended by chromosome disturbances.

10. In my experiments, water treated series give a lower value of

mutation and mutant frequencies than untreated series. The macromutations and especially the macromutations of *alboviridis* show a deficiency in the water treated series. The conclusion is drawn that the *alboviridis* mutations chiefly arise in those nuclei which have a high water content and which in consequence give more chromosome aberrations and are more easily killed.

11. The five types of mutation have different selective values. In the oldest seed series, used for X raying, mainly *albina* mutations arise. The cause of that is probably that these mutations, as postulated above, are attended by smaller changes in the genotype than the other types of mutation.

12. Micromutations arise more readily in dry than in damp nuclei of fresh seed series. In proportion as the seed series grow older the effect of this environmental factor is outbalanced by morbid phenomena of old age in the genes. As wet seeds of old series have changed to a greater extent than corresponding dry series the number of micromutations is higher in the former.

13. In spite of the great change of the chromosomes with the ageing of the seeds fewer genetically discernible chromosomal aberrations (macromutations) appear. In other words, the chromosomal aberrations become so potent that they are eliminated to a greater extent during ontogenesis than in fresh caryopses.

14. On the basis of the experimental results, the different genetic size of the chlorophyll mutations is discussed on pp. 85—89.

Svalöf, June 1st, 1937.

LITERATURE CITED.

1. Brunson, A. M. 1924. The Inheritance of a Lethal Pale Green Seedling Character in Maize. — Corn. Univ. Agr. Exp. Stat. Mem. 72.
2. Cartledge, J. L. and Blakeslee, A. F. 1934. Mutation Rate Increased by Aging Seeds as Shown by Pollen Abortion. — Proc. Nation. Acad. Sciences, Vol. 20.
3. Collins, J. L. 1927. A Low Temperature Type of Albinism in Barley. — Journ. of Hered. 18.
4. de Haan, H. 1933. Inheritance of Chlorophylldeficiences. — Bibl. Gen. 10.
5. Demerec, M. 1923. Inheritance of White Seedlings in Maize. — Genetics 8.
6. — 1924. Genetic Relations of Five Factor Pairs for Virescent Seedlings in Maize. — Corn. Univ. Agr. Exp. Stat. Mem. 84.
7. — 1925. Inheritance of Pale Green Seedlings in Maize. — Genetics 10.
8. — 1926. Notes on Linkage in Maize. — Amer. Natur. 60.

9. DEMEREC, M. 1935 a. Behaviour of Chlorophyll in Inheritance. — Cold Spring Harbor Symposia of Quantitative Biology, Vol. 3.
10. — 1935 b. Role of Genes in Evolution. — Amer. Natur. 69.
11. EYSTER, W. H. 1934. Genetics of *Zea Mays*. — Bibl. Gen. 11.
12. GUSTAFSSON, Å. 1936. Über verschiedene Stabilität und Sensibilität der Chromosomen. — Bot. Not.
13. — 1937 a. The Different Stability of Chromosomes and the Nature of Mitosis. — Hereditas XXII.
14. — 1937 b. Der Tod als ein nuklearer Prozess. — Hereditas XXIII.
15. HALLQVIST, C. 1923. Gametenelimination bei der Spaltung einer zwerghaften und chlorophylldefekten Gerstensippe. — Hereditas IV.
16. — 1924. Chlorophyllmutanten bei Gerste. — Hereditas V.
17. — 1926—1927. Koppelungen und synthetische Letalität bei den Chlorohpyll-faktoren der Gerste. — Hereditas VIII.
18. JENKINS, M. T. 1926. A Second Gene Producing Golden Plant Colour in Maize. — Amer. Natur. 60.
19. JENKINS, M. T. and BELL, M. A. 1930. The Inheritance, Interactions and Linkage Relations of Genes Causing Yellow Seedlings in Maize. — Genetics 15.
20. KANNA, B. 1935. Chlorophyll Deficient Rice Seedlings Induced by X Rays. — Journ. Coll. Agr. Tokyo Imp. Univ. 13.
21. KARPER, R. E. and CONNER, A. B. 1931. Inheritance of Chlorophyll Characters in *Sorghum*. — Genetics 16.
22. LINDSTROM, E. W. 1918. Chlorophyll Inheritance in Maize. — Corn. Univ. Agr. Exp. Stat. Mem. 13.
23. — 1924. Complementary Genes for Chlorophyll Development in Maize and their Linkage Relations. — Genetics 9.
24. — 1925. Genetic Factors for Yellow Pigment in Maize and their Linkage Relations. — Genetics 10.
25. MILES, F. C. 1915. A Genetic and Cytological Study of Certain Types of Albinism in Maize. — Journ. of Gen. 4.
26. MORINAGA, T. 1932. The Chlorophyll Deficiences in Rice. — Bot. Mag. 46.
27. MULLER, H. J. 1932. Further Studies on the Nature and Causes of Gene Mutations. — Proc. sixth Intern. Congr. Gen. Vol. 1.
28. NAVASHIN, M. and GERASSIMOVA, H. 1935. Nature and Causes of Mutations. I. On the Nature and Importance of Chromosomal Mutations Taking Place in Resting Plant-Embryos Due to their Ageing. — Zschr. f. Biol. IV.
29. NILSSON, HERIBERT. 1915. Die Spaltungserscheinungen der *Oenothera Lamarckiana*. — Lunds Univ. Årsskr. N. F. Avd. 2, 12.
30. — 1920. Zuwachsgeschwindigkeit der Pollenschläuche und gestörte Mendelzahlen bei *Oenothera Lamarckiana*. — Hereditas I.
31. — 1931. Sind die induzierten Mutanten nur selektive Erscheinungen? — Hereditas XV.
32. NILSSON-EHLE, H. 1921. Über mutmassliche partielle Heterogamie bei den Speltoidmutationen des Weizens. — Hereditas II.
33. — 1922. Über freie Kombination und Koppelung verschiedener Chlorophyll-erbeinheiten bei Gerste. — Hereditas III.

34. PHIPPS, I. F. 1929. Inheritance and Linkage Relations of Virescent Seedlings in Maize. — Corn. Univ. Agr. Exp. Stat. Mem. 125.
35. ROBERTSON, D. W. 1929. Linkage Studies in Barley. — Genetics 14.
36. SCHICK, R. und STUBBE, H. 1932. Die Gene von *Antirrhinum majus*. — Zschr. f. ind. Abst.- u. Vererb.-lehre 62.
37. SHULL, G. H. 1913. Über die Vererbung der Blattfarbe bei *Melandrium*. — Ber. deutsch. Bot. Ges. 31.
38. SIRKS, M. J. 1932. Beiträge zu einer genotypischen Analyse der Ackerbohne, *Vicia Faba*. — Genetica 13.
39. STROMAN, G. N. 1924. Genetic Relations of Chlorophyll and Anthocyanin Seedling Characters in Maize. — Genetics 9.
40. STUBBE, H. 1935. Weitere Untersuchungen über Samenalter und Genmutabilität bei *Antirrhinum majus*. — Zschr. f. ind. Abst.- u. Vererb.-lehre 70.
41. TIMOFÉEFF-RESSOVSKY, N. W., ZIMMER, K. G. und DELBRÜCK, M. 1935. Über die Natur der Genmutation und der Genstruktur. — Nachr. d. Gesellsch. d. Wiss. zu Göttingen, Fachgr. VI, Bd. I, Nr. 13.
42. TRAJKOVICH, H. 1924. Inheritance of Xantha Seedlings in Maize. — Corn. Univ. Agr. Stat. Mem. 82.
43. WIEBE, G. A. 1924. Albinism in Barley. — Journ. of Hered. 15.

CONTENTS.

I. Introduction 33
II. Material and methods 34
III. The genetic basis of chlorophyll formation 37
1. The range of the induced chlorophyll mutations 37
2. The fertility of ears with induced chlorophyll mutations 38
3. The segregation conditions in spontaneous chlorophyll mutations in barley 43
4. Chlorophyll mutations in other species of plants 48
5. Synthetic lethality in barley and its causes 53
6. Segregation aberrations in induced mutations 56
7. Changes in the types of mutation in ageing 58
IV. Segregation aberrations due to gamete elimination 59
V. The mechanism of induced mutating 67
1. Water content, type of mutation and frequency of mutations 67
2. Water content, age and micromutations 75
3. Age and frequency of mutations 80
4. Age and type of mutation 83
VI. The different genetic size of chlorophyll mutations 85
Summary 89
Literature cited 91

A PECULIAR ASYMMETRICAL MITOSIS IN THE MICROSPORE OF ORCHIS

BY *O. HAGERUP*
BOTANICAL MUSEUM, COPENHAGEN

WHEN studying the pollen development of our *Orchis* species I have often, in order to estimate the chromosome numbers, also studied the later cell divisions in the microspores. On that occasion I noticed, however, a peculiar asymmetrical mitosis. I have searched the literature to find descriptions of similar conditions, but in vain. Hence I am compelled to assume that this has not hitherto been known, and I request other investigators to observe whether a similar asymmetrical mitosis also occurs during the first division of the microspore in other plants. The second mitosis, by which two male gametes are formed, is not, on the other hand, asymmetrical. All the observed *Orchis* species behave essentially in the same way in respect to the conditions mentioned here.

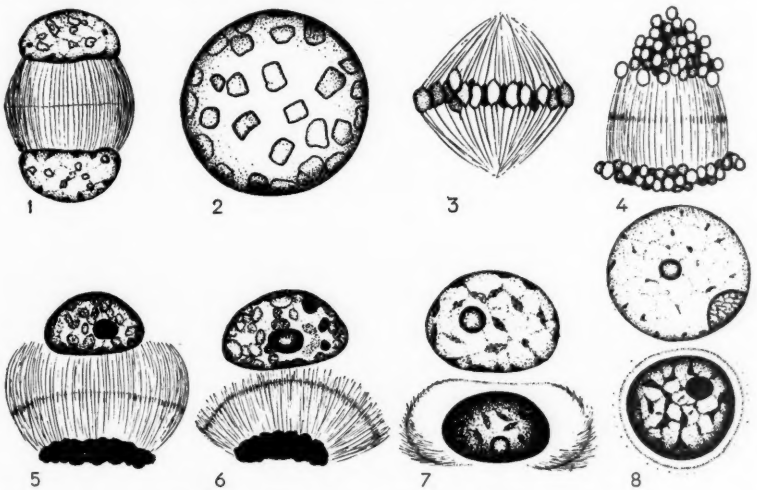
It is especially the spindles which should be subjected to a closer investigation. These are best observed after fixing in fluids containing chromic acid (not Carnoy's fixative), and they become distinct when deeply stained according to Heidenhain.

First it should be emphasized that the reduction division itself is quite normal. The mitoses are symmetrical as in most other plants. Therefore the appended Fig. 1 will suffice; it shows a typical interkinesis. All the figures, 2—8, show a continuous series of phases from the incipient germination of the microspore. It begins by being uninucleate (Fig. 2) and ends by being binucleate (Fig. 8), like so many other ripe pollen grains in the phanerogams; finally, a larger »vegetative nucleus» is observed and a smaller, dark, generative nucleus. The other parts of the pollen grain (wall and plasm) have not been drawn in the figures.

Even one of the first division phases of the germinating microspore (Fig. 2) is peculiar, in that it resembles a diakinesis with short and broad gemini. The succeeding metaphase (Fig. 3) is quite normal, but already in the young telophase (Fig. 4) it is plainly seen that the two young daughter cells are not identical, the chromosomes grouping themselves in different ways. Only the group of chromosomes, which

become the generative nucleus, arrange themselves in an almost *plane* surface, in contrast with the chromosomes of the vegetative nucleus, which assemble in an almost hemispherical group (see Fig. 4, above). Corresponding to this dissimilar grouping of the chromosomes, the spindle fibres, too, distribute themselves in a similar asymmetrical way, and now the first faint indication of a wall between the two daughter nuclei is also seen.

As soon as the daughter nuclei have become so old that they have surrounded themselves with a membrane (Fig. 5), the most peculiar



Figs. 1—8. *Orchis maculatus.* — Fig. 1. Interkinesis (1440/1). — Figs. 2—8. The first mitosis in the germinating microspore. Note especially the behaviour of the spindle fibres. — Fig. 8. The nuclei of a ripe pollen grain. (2880/1). Cp. also the text.

occurrence in the whole cell division takes place, however. The spindle fibres begin to disengage themselves from the vegetative nucleus (Fig. 5), while still adhering to the generative nucleus. First the peripheral spindle fibres become detached (Fig. 5), and soon they are all loosened (Fig. 6) from the vegetative nucleus and spread sideways so that they surround the generative nucleus like an apparently fan-shaped figure, which, however, is uniformly circular in transverse section. This fan (Fig. 6) steadily unfolds itself more and more sideways (Fig. 7) and at the same time it looks as if the spindle fibres contract and disappear in a characteristic way as shown in Fig. 7. At the same time the newly

formed cell wall becomes more and more distinct and surrounds the generative nucleus like an almost hemispherical cap (Fig. 7), which finally becomes an even layer round the whole of the generative nucleus within the ripe pollen grain (Fig. 8).

Some of the changes taking place simultaneously in the two nuclei are shown in the figures. It is, however, of special interest to note the difference in the principle of the development of the two nuclei, and to compare this difference with the subsequent widely different functions of the nuclei. It may perhaps be of importance for studies on the sexual problem to know that *a neutral cell (the vegetative cell) has received nothing whatever from the spindle fibres, but that these, even in a double dose, fall to the cell which is to act as the mother cell of the reproductive cells.* The possibility that the spindle fibres might have some sexual significance should therefore be kept in mind in future investigations.

Unfortunately I have not been able to decide what part the peculiar layer formed by the spindle fibres round the generative nucleus plays during the germination of the pollen and during the fertilisation; but perhaps questions of fundamental interest may be involved here, as, for instance, whether the possibility should also be taken into account of a plasmatic inheritance through the *male* reproductive cells, etc.?

SUMMARY.

The subjoined Figs. 2—8 show that the first mitosis in the germinating microspore (in *Orchis*) is conspicuously asymmetrical. The spindle fibres become detached from the vegetative nucleus; they go exclusively to the generative nucleus and surround it like a special layer.

ANAGALLIS ARVENSIS L. *s. l.* UND DIE NATUR IHRER FARBENVARIANTEN

VON *HERIBERT NILSSON*
BOTANISCHES INSTITUT, LUND

VON *Anagallis arvensis* L. wurden schon früh vom normalen rotblühenden Typus abweichende Formen beobachtet. So erwähnt LINNÆUS in seiner Species plantarum 1753 eine blaublühende Art, *A. latifolia*, auf die ich später zu sprechen komme. SCHREBER beschreibt 1771 eine blaublühende *Anagallis*-Art als *A. coerulea*. Die blaue Blütenfarbe erschien offenbar so auffallend, dass man diese Variante als artverschieden betrachtete. Man suchte deshalb auch nach anderen Charakteren, die diese Unterscheidung bestätigen sollten.

Charaktere, die nach der floristischen Literatur *A. coerulea* SCHREB. von *A. arvensis* L. abgrenzen sollten, sind, ausser der blauen Blütenfarbe: Krone am Rande kahl oder spärlich drüsig-bewimpert (bei *arvensis* reich), Kronenblätter am Rande ausgebissen gesägt (bei *arvensis* ganzrandig), Kelchblätter am Rande feingesägt (bei *arvensis* ganzrandig), Blütenstiele von der Länge des stützenden Blattes (bei *arvensis* länger), Blätter oberhalb der Mitte scharf verjüngt (also spitzer als bei *arvensis*), die ganze Pflanze von üppigerer Wuchsform als *arvensis*.

Obgleich also mehrere Charaktere als distinkte Differenzen für *A. coerulea* SCHREB. angegeben wurden, so wurde die Art doch von mehreren floristischen Forschern nicht als selbständige Art anerkannt, und bis auf den heutigen Tag bestehen in dieser Hinsicht Meinungsverschiedenheiten. Einen Ausdruck für die streitige Auffassung um die Mitte des neunzehnten Jahrhunderts findet man in einer Äusserung von GÄRTNER, der selbst auch mit *Anagallis* experimentiert hatte. Er sagt (1849, p. 309): »Wir haben uns vielfach vergeblich bemüht, die *Anagallis phoenicea* mit der *coerulea* und umgekehrt zu befruchten, welches, wenn sie, wie WILLDENOW, WIEGMANN und TRATTINIK behauptet haben, blosse Varietäten wären, leicht erfolgen würde, übrigens haben schon CH. GMELIN, SCHRANK, VOITH und KOCH die specifische Verschiedenheit dieser beiden Pflanzen nachgewiesen».

GÄRTNER ist also der Ansicht, dass *A. coerulea* SCHREB. eine distinkte Spezies ist, speziell weil er zwischen dieser Art und *A. arvensis* L. (*phoenicea* SCOP.) Inkompatibilität gefunden hat.

Kulturversuche und Kreuzungen zwischen diesen Farbentypen sind auch einige Jahrzehnte später von H. HOFFMANN vorgenommen worden. Er arbeitete mit noch einer Farbenform, die er *A.* (*coerulea*? var.) *rosea* nannte. Er fand sie mehrmals in Samenproben aus botanischen Gärten. Dieser Farbentypus ist gewiss zu einem von SCHRANK beschriebenen synonym (1789, p. 461), der als Subspezies zu *A. coerulea* SCHREB. als **carnea* SCHRANK gesetzt wird. Seine Versuche sind in grossem Massstabe während zwanzig Jahren (1867—1886) fortgesetzt worden, brachten aber keine vollständige Klarheit in bezug auf ihre Variabilität und Distinktion. Sein Hauptresultat fasst er wie folgt zusammen (1887, p. 26): »Alle drei Farben können umschlagen; die rote ist die festeste und züchtete in einzelnen Serien vollkommen rein; etwas schwächer vererbt die *rosea* und *coerulea*». — »Dies spricht nicht», sagt er, »für spezifische Verschiedenheit» (1879, p. 181). Er hat auch versucht, künstliche Kreuzungen auszuführen, diese sind aber, wie die von GÄRTNER, misslungen, was seine Resultate noch ungewisser macht.

Weder GÄRTNERS noch HOFFMANNS Kulturversuche und Kreuzungen haben die Frage von der Natur der Farbenvarianten entschieden. Noch eine Versuchsserie in bezug auf diese liegt indessen vor, nämlich von FOCKE. In seiner berühmten Arbeit, Pflanzen-Mischlinge (1881), berichtete er auch über *Anagallis*-Bastarde. Bei Kreuzung von *phoenicea* (*arvensis*) × *coerulea* und reziprok erhielt er einen roten Bastard, der in der Nachkommenschaft sowohl rote als blaue Pflanzen lieferte. Der Bastard war also rot, *nicht rosa*, wie man vielleicht vermuten könnte und auch vermutet hatte. In dieser Hinsicht war der Versuch klärend, was nicht hinderte, dass man die rosafarbige Form fortwährend für einen Bastard zwischen *A. arvensis* L. und *A. coerulea* SCHREB. hielt, wie ich unten weiter auseinandersetzen werde.

HOFFMANN erhielt von FOCKE Samen seines artifiziellen Bastards. Diese lieferten 49 rotblütige und 6 blaublütige Pflanzen. Bei Aussaat von Samen der blauen, erhielt er »neben mehrere blauen 2 rothe und 5 rosafarbig blühende Pflanzen». »Die Variabilität ist also», schliesst er, »gerade so, wie bei den unzweifelhaft nicht hybriden Culturen». Rosa kam also in der Bastardnachkommenschaft hervor. FOCKES klares Resultat wurde durch HOFFMANNS »Nachprüfung» nur getrübt, und die Frage der Natur der Farbenvarianten wieder ganz unsicher gemacht. Hierzu trug gewiss auch bei, dass FOCKE über Pollensterilität des Bastards spricht. Die Hälfte der Pollenkörner waren missgestaltet. Da man schlechten Pollen als einen guten Indikator für Artdifferenz betrachtete, schienen *A. arvensis* L. und *A. coerulea* SCHREB. wirklich

differente linnéische Arten zu sein. Der Bastard fiel aber nicht intermediär aus, wie in diesem Fall zu erwarten gewesen wäre. Die Fruchtbarkeit war auch ganz normal. Eine Übersicht sämtlicher Tatsachen gab keine entscheidende Antwort in bezug auf die Frage, ob die betreffenden Elternformen als Arten oder Farbenformen zu betrachten wären.

Da das Experiment keine Klärung gebracht hatte, ist es kaum erstaunenswert, dass der Streit der Taxonomisten fortsetzte. LINNÉ hatte, wie oben erwähnt, eine blaublühende Form als *A. latifolia* beschrieben. Er zitiert TOURNEFORTS Diagnose: »Anagallis hispanica latifolia, maximo flore», und gibt für ihre Verbreitung nach LOEFLING an: »Habitat in Hispania». MILLER (1768) nimmt die Art in seinem bekannten Gartenlexikon mit der linnéischen Beschreibung auf. Er erwähnt, dass er sie aus Spanien von dem Oberaufseher der königlichen Gärten zu Madrid, HORTEGA, erhalten habe. Neben dieser blaublühenden Art führt er *A. femina* (*coerulea*) als neue Spezies auf.

In der vierten Ausgabe von Species plantarum führt der Herausgeber, WILLDENOW, die von SCHREBER 1771 beschriebene *A. coerulea* nur als eine Varietät der *A. arvensis* L. an. Diese Art wird in *α A. flore coeruleo* und *β A. phoeniceo flore* aufgeteilt. Zu der Art setzt er folgende Bemerkungen: »Licet corollae color in A. arvensi et coerulea cultura non mutetur, tamen melius fore eas conjungere, quum characteres specifici nimis sint artificales, existimavi». Von *A. arvensis* L. sagt er weiter: »Var. *β* variat flore albo, umbilico purpureo». Wahrscheinlich zielt er hiermit auf die *carnea*-(*rosea*-)Form ab, zitiert aber nicht SCHRANK, sondern POLLICH (1776).

POLLICH stellt von *A. arvensis* L. drei Varietäten auf: *α Anagallis phoeniceo flore*; *β Anagallis coeruleo flore*; c. Flore albo quoque observavi, umbilico purpureo. Hier werden wohl zum ersten Mal die drei ausgeprägten Farbenvarianten als gleichwertige Varietäten angeführt, denn var. c. ist gewiss *carnea*, was das Erwähnen des purpurnen Grundes der Blütenkrone wahrscheinlich macht. Diesem gegenüber erscheinen die freien Teile der Kronenblätter weiss (hellrosa oder hellila).

A. latifolia L. führt WILLDENOW wie LINNÉ als Spezies auf, bemerkt aber: »Notabilis foliis magnis et latis, caule compresso, A. arvensi attamen valde affinis». Auch über den Spezieswert jener Art ist er also sehr im Zweifel. Diese Art wurde von LANGE bei seiner spanischen Reise (1851—1852) als eine blaublütige *A. arvensis* L. angehörige Form identifiziert. Sie wird als ein mediterraner Typus betrachtet, der grössere Blüten und kräftigeren Wuchs hat. LANGE stellt also keine blaublütige

Art oder Varietät auf, sondern meint, dass *A. arvensis* L. rot- oder blaublütig sein kann (WILLKOMM et LANGE, 1870, p. 648). Darin stimmt seine Auffassung mit der von LINNÉ überein, dass *A. latifolia* L. als habituell abweichender Typus eine beachtenswertere Form als eine Farbenform ist. Sie wird indessen nicht als Art betrachtet, sondern als Varietät. Er führt sie als *A. arvensis β latifolia* LANGE auf. Der Riesenwuchs dieser Varietät scheint darauf zu deuten, dass sie eine Polyploide ist. Ob sie mehr als eine weit verbreitete alte Gartenform aus Spanien ist, ist wohl noch unsicher.

Auch in den neueren floristischen Arbeiten ist die Auffassung der Farbentypen von *A. arvensis* L. sehr verschieden. In KOCHS Synopsis, III. Aufl. (1907) werden die Arten *A. arvensis* L. und *A. coerulea* SCHREB. aufgenommen, während *carnea* nicht einmal als Varietät vorkommt; unter *A. arvensis* werden nur von der gewöhnlichen mennigroten Blütenfarbe abweichende Nuancen erwähnt: weiss, am Grunde blutrot; oder ganz fleischrot oder lila oder violett. In HEGI (1926) wird von LÜDI, der die Gattung bearbeitet hat, die rote und die blaue Form als subsp. *phoenicea* (SCOP.) GREN. et GODR. und subsp. *coerulea* (SCHREB.) GREN. et GODR. angeführt, ferner unter letzterer die var. *latifolia* (L.) LANGE. Die rosafarbige Form (*carnea*) wird als synonym zu *phoenicea* × *coerulea* gestellt. In ENGLERS Pflanzenreich (1905) werden von KNUTH *phoenicea*, *coerulea* und *latifolia* als Varietäten betrachtet, *carnea* als Bastard *phoenicea* × *coerulea*. Die Ansichten der Verfasser dieser floristischen Hauptwerke gehen also weit auseinander.

Die Vermutung, dass *carnea* eine Bastardform zwischen *phoenicea* und *coerulea* sei, was aber sowohl durch HOFFMANNS Kulturversuche als durch FOCKES Kreuzungsresultat widerlegt worden ist, taucht also in diesem Jahrhundert wieder auf. Die Ursache hierfür scheint zu sein, teils eine Distribuierung von *carnea* unter der Bezeichnung *A. arvensis* × *coerulea* durch DÖRFLER (1903), teils eine Angabe von RUNDKWIST (1914), dass er bei Kreuzung der betreffenden Farbenformen als Resultat eine rosafarbige Form erhalten habe. Im Herbarium des Bot. Museums zu Lund liegen die Originalexemplare sowohl seines vermuteten spontanen Bastards aus Vedeby (Schweden) als seines artifiziellen Bastards, den er 1914 beschrieben hat. Die Blüten sind gewiss rosafarbig. Diese Pflanzen können aber nicht Bastarde zwischen *arvensis* und *coerulea* sein. Denn wie oben dargetan, hat FOCKE eine rotblütige F_1 und in F_2 Spaltung in Rot und Blau gefunden. WEISS, der auch diesen Bastard hergestellt hat (1911), erhält ganz dasselbe Resultat. Wie ich unten ausführlich zeigen werde, sind ihre Resultate richtig.

RUNDKWISTs Resultat muss auf einen Versuchsfehler beruhen. Wie man dieses zu deuten hat, werde ich unten, nach Besprechung meiner Kreuzungen, wahrscheinlich machen.

Während mehreren Jahren habe ich Versuche mit den hier behandelten Farbenformen von *A. arvensis* L. sens. lat. ausgeführt. Die Ursache war das Auffinden einer rosafarbigen Form in Hörte in Schweden. Sie war bei Vermehrung konstant, und ergab bei Kreuzung mit rotblütig rotblütige F_1 und monohybride Mendelspaltung in F_2. Die Form ist sicher mit *A. *carnea* SCHRANK identisch. Über diese Versuche habe ich schon 1912 berichtet. Später habe ich auch die Kreuzungen Rot × Blau und Rosa × Blau ausgeführt, und meine Versuche sind so umfassend geworden, dass man eine klare Übersicht über die Natur der betreffenden Farbenvarianten erhält.

TABELLE 1. *Spaltung phoenicea × carnea (Rot × Rosa).*

F_2			F_3			F_4			
Nr.	Rot	Rosa	Nr.	Rot	Rosa	Nr.		Rot	Rosa
I	18	9	2—12	12	5	17—13		5	3
II	127	45	30—12	47	15	18—13		6	2
III	33	11	31—12	17	2	19—13		7	2
						20—13	Aus 30—12	6	1
						22—13		38	7
						23—13		25	9
						26—13		12	1
	178	65		76	22			99	25

Gefundene Spaltung für F_2, F_3 und F_4 ..... 353 : 112
Erwartet ..... 348,75 : 116,25 ± 9,35

Da die Differenz zwischen Gefunden und Erwartet nur 4,25 beträgt, der mittlere Fehler 9,35, zeigt die Spaltung eine sehr gute monohybride Verteilung der Farbenvarianten Rot und Rosa, oder, was ganz dasselbe ist, der *phoenicea*- und *carnea*-Typen von *Anagallis arvensis* L.

Diese Spaltung wird auch durch die Verteilung spaltender und konstanter Nachkommenschaften in F_3 und F_4 bestätigt. Wie aus Tabelle 1 ersichtlich ist, war die Zahl der spaltenden Nachkommenschaften 10. Konstant waren in F_3 3 und in F_4 auch 3 Nachkommenschaften. Die Verteilung 10 : 6 stimmt also mit dem erwarteten Verhältnis 2 : 1 sehr gut überein.

Um auch die übrigen Farbenverbindungen zu prüfen, führte ich eine Kreuzung zwischen einer Pflanze der Nachkommenschaft 23—13,

die rotblütig war (23 a—13), und *coerulea* aus. Die letzte war nicht schwedischer Herkunft, sondern wurde als Samenprobe (5—13) aus dem Botanischen Garten in Nantes erhalten. Die verwendete Pflanze wurde mit 5 a—13 bezeichnet.

Die *phoenicea*-Pflanze war eine Bastardpflanze, wie schon die Spaltung in F_1 zeigte. Diese war nämlich 14 Rot : 19 Rosa.

Alle diese Pflanzen müssen nun Bastarde mit Blau sein, bei den ersten soll eine Spaltung in Rot und Blau (*phoenicea* und *coerulea*), bei den letzten in Rosa und Blau (*carnea* und *coerulea*) eintreten.

TABELLE 2. *Spaltung phoenicea* × *coerulea* (*Rot* × *Blau*).

F_2				F_3			
Nr.	Rot	Blau	Rosa Vizinisten	Nr.	Rot	Blau	Rosa Vizinisten
6—15	72	21	3	1—16	46	15	—
7—15	25	7	1	4—16	59	22	—
8—15	16	4	1	5—16 Aus	117	46	—
9—15	19	4	—	6—16 10—15	56	28	—
10—15	56	15	4	7—16 Aus	48	9	—
11—15	26	5	2	9—16 13—15	43	6	—
13—15	45	14	1	8—16 Aus 15—15	61	21	—
15—15	43	11	1				
16—15	44	18	2				
19—15	22	6	—				
20—15	17	5	—				
21—15	54	21	3				
22—15	33	6	2				
23—15	11	3	1				
	483	140	21		430	147	—

Für F_2 und F_3 zusammengenommen erhält man also die Spaltung .... 913 : 287
Erwartet ..... 900 : 300 ± 15

Die vierzehn roten Pflanzen ergaben in F_2 und F_3 obenstehende Spaltungszahlen (Tab. 2).

Auch diese Spaltung ist sehr gut, da die Differenz nicht einmal den einfachen mittleren Fehler erreicht. Die Verteilung der Varianten *phoenicea* und *coerulea* ist also klar monohybrid mit Dominanz von *phoenicea.*

Die neunzehn rosafarbigen Pflanzen aus der oben erwähnten Kreuzung *phoenicea* (23 a—13) und *coerulea* (Nantes) ergaben folgende Spaltung in F_2 und F_3 (Tab. 3).

Diese Spaltung zeigt gute monohybride Verteilung der Varianten, denn die Differenz beträgt nur das 1,5-fache des mittleren Fehlers. Auch die *carnea*- und *coerulea*-Formen geben also eine einfache Mendelspaltung mit Dominanz von *carnea*.

Noch eine Kreuzung zwischen *carnea* und *coerulea* wurde ausge-

TABELLE 3. *Spaltung carnea* × *coerulea* (*Rosa* × *Blau*).

F_2				F_3			
Nr.	Rosa	Blau	Rote Vizinisten	Nr.	Rosa	Blau	Rote Vizinisten
12—15	7	4	—	21—16 Aus	82	16	—
14—15	48	10	—	22—16 41—15	68	26	—
17—15	19	4	1	33—16	50	16	—
18—15	14	6	—	35—16 Aus	64	27	—
41—15	110	30	4	36—16 49—15	46	6	—
42—15	104	33	6	37—16	10	4	—
43—15	71	32	4				
44—15	148	47	3				
45—15	69	17	4				
47—15	35	4	3				
48—15	29	9	1				
49—15	92	23	3				
50—15	37	16	—				
51—15	51	17	2				
52—15	43	18	2				
53—15	26	8	—				
54—15	4	—	—				
55—15	—	1	—				
56—15	—	—	—				
	907	279	33		320	95	

Für F_2 und F_3 zusammengenommen erhält man also die
Spaltung ..... 1227 : 374
Erwartet ..... 1200,75 : 400,25 ± 17,33

führt, nämlich zwischen einer rosafarbigen Pflanze der Nachkommenschaft 23—13, aus der auch die für die letzterwähnte Kreuzung benutzte Mutterpflanze stammte (23 a—13). Die rosafarbige Mutterpflanze (23 b—13) wurde mit derselben *coerulea*-Pflanze (5 a—13) gekreuzt wie 23 a—13. Hier wurde die Kreuzung *carnea* × *coerulea* direkt ausgeführt, während die oben in Tab. 3 referierte ja indirekt erhalten wurde [durch Kreuzung (*phoenicea* × *carnea*) × *coerulea*]. Das Resul-

tat war, dass sämtliche 19 F_1-Pflanzen rosablütig waren. In F_2 und F_3 wurde folgende Spaltung erhalten (Tab. 4).

Die Spaltung ist sehr gut, die Differenz liegt innerhalb des einfachen mittleren Fehlers. Diese Kreuzung verifiziert das Resultat der früheren Kreuzung (Tab. 3), nämlich dass auch die Verbindung *carnea* × *coerulea* (Rosa × Blau) eine monohybride Mendelspaltung zeigt.

TABELLE 4. *Spaltung carnea* × *coerulea* (*Rosa* × *Blau*).

F_2				F_3			
Nr.	Rosa	Blau	Rote Vizinisten	Nr.	Rosa	Blau	Rote Vizinisten
1—15	39	11	1	14—16 Aus 28—15	46	18	—
2—15	140	41	—	15—16	130	35	—
3—15	33	11	—	16—16	121	48	—
4—15	81	21	—	17—16	70	27	—
5—15	13	8	—	18—16	37	8	—
24—15	53	17	—				
25—15	118	29	—				
26—15	45	28	—				
27—15	88	24	—				
28—15	71	18	—				
29—15	78	29	—				
30—15	85	27	—				
31—15	46	20	1				
32—15	27	6	—				
33—15	28	10	—				
34—15	52	27	—				
35—15	13	4	—				
36—15	49	10	—				
37—15	33	6	—				
	1092	347	2		404	136	—

Für F_2 und F_3 zusammengenommen erhält man also die Spaltung ..... 1496 : 483
Erwartet ..... 1484,25 : 494,25 ± 19,39

Betreffs der Spaltungen mag es auffallend erscheinen, dass ausser den behandelten beiden Spaltungsklassen einer Kreuzung noch eine dritte und unerwartete Klasse aufgetreten ist. In Tab. 2 treten zum Beispiel in der Kreuzung Rot × Blau in F_2 einzelne rosafarbige Pflanzen auf. Es hat den Anschein, als ob Rosa hier in geringem Prozentsatz ausspaltete. Das ist indessen nicht der Fall. Betrachtet man statt

F_2 die F_3 derselben Tabelle, so sieht man, dass hier eine Spaltung nur in Rot und Blau stattfindet. Die Ursache dieses Unterschieds ist indessen, dass im ersten Fall eine ungewollte Bestäubung eingetreten ist. *A. arvensis* ist ein fast obligater Selbstbefruchter, indem der Pollen schon in der Knospe die Staubbeutel verlässt und die Befruchtung ausführt. Unter gewissen Verhältnissen, bei häufigerem Insektenbesuch, können die fremden Pollenkörner vereinzelt eine Befruchtung erzielen, und es resultiert eine ungewollte Befruchtung (Vizinismus). Wird in dem behandelten Fall eine Bastardpflanze Rot × Blau für Vizinismus mit Pollen von Rosa ausgesetzt, so müssen in der Nachkommenschaft einzelne Pflanzen mit rosafarbigen Blüten auftreten, denn in der Verbindung Blau × Rosa dominiert, wie oben dargetan, Rosa.

Die Ausgangspflanzen (F_1) von Tab. 2 und 3 wurden nicht im Freien, sondern in Töpfen in einem sonnigen Zimmer aufgezogen. Wahrscheinlich sind sie hier von ziemlich stationären Insekten, vielleicht Fliegen, besucht worden. Der Prozentsatz von Vizinisten ist nämlich ganz ungewöhnlich hoch und beträgt sowohl in Tab. 2 wie 3 ungefähr 3 %. In Tab. 3, in der Kreuzung Rosa × Blau, sind die Vizinisten natürlich rot.

In F_3 der betreffenden Kreuzungen findet sich kein einziger Vizinist, obgleich die Individuenzahl zusammen fast 1000 beträgt. Die Ausgangspflanzen der F_3 blühten indessen im Freien ab. Der Insektenbesuch ist hier gewiss sehr spärlich, die Selbstbefruchtung wird vollkommen. In den Nachkommenschaften in Tab. 4 ist der Vizinismus auch sehr spärlich. Unter 2000 Pflanzen finden sich nur 2 Vizinisten, also nur 1 pro mille. Der Grad des Vizinismus ist offenbar variabel und von den Bedingungen des Abblühens abhängig.

Der von mir konstatierte Vizinismus ist insofern von Bedeutung, als er die Ursache der höchst merkwürdigen Resultate von HOFFMANN erklärt. Er fand ja in seinen zwanzigjährigen Kulturen, dass die Farbenvarianten in jeder Richtung aus einander hervorgehen können. Die Ursache dieses Resultats ist Vizinismus und Spaltung. Ist z. B. eine *coerulea*-Pflanze für Vizinismus von Rot und Rosa ausgesetzt worden, so muss sie, falls sie als Mutterpflanze ausgewählt wird, neben blauen auch einzelne rote und rosa Pflanzen geben, weil diese Eigenschaften über Blau dominieren. Und umgekehrt müssen diese roten und rosa Vizinisten, falls sie als Mutterpflanzen ausgewählt werden, in den Nachkommenschaften blaue Pflanzen geben. HOFFMANNS Resultate sind also durch das stetige Nebeneinanderbauen der Kulturen und des hier-

durch verursachten Vizinismus mit darauffolgender Spaltung ganz verständlich.

RUNDKWIST hat, wie oben erwähnt (S. 100), ganz eigentümliche Resultate erhalten, indem F_1 aus Rot × Blau Rosafarbig und in F_2 Spaltung in Rosa, Rot und Blau gezeigt haben sollte. Wie meine umfassenden Versuche zeigen, trifft dies gar nicht zu. Es muss ein Versuchsfehler vorgelegen haben. Die Sachlage ist folgende. Er fand rosablütige Pflanzen wildwachsend und deutete sie als Bastarde. Da er keine Nachkommenschaft aufgezogen hat, ist die Bastardnatur nicht erwiesen. Diese Pflanzen waren sicher nur die *carnea*-Form von SCHRANK.

Dann hat er auch die Kreuzung Blau × Rot ausgeführt, wobei eine rosa F_1 erhalten worden ist. Dieses Resultat kann man vielleicht folgendermassen erklären. Bei der Kreuzung wurde *coerulea* als Mutter benutzt. Wahrscheinlich hat ein Verwechslung mit oder Verunreinung durch *carnea*-Pollen bei der Kreuzung stattgefunden, weshalb die »Bastarde» Rosafarbig wurden. Diese F_1-Pflanzen konnten, im Freien unter roten *arvensis*-Pflanzen stehend, von diesen für Vizinismus ausgesetzt werden. Der »Bastard» musste dann in Rosa, Rot und Blau spalten.

Das *Gesamtresultat* meiner oben behandelten Kreuzungen ist also, dass *sämtliche Farbenvarianten, phoenicea, carnea* und *coerulea, bei Kreuzung unter sich monohybride Spaltung aufweisen.* Dies bedeutet, dass sie nur in bezug auf einen einzigen erblichen Faktor different sein können, d. h., sie sind nur ganz einfache Varianten in bezug auf das Farbenmerkmal, wie man sie z. B. bei den Kulturpflanzen zahlreich antrifft. Als Arten können sie gar nicht aufgefasst werden. Die Bastarde *sind morphologisch nicht sichtbar.* Ihre Fertilität ist ebenso gut wie die der Elternformen.

Von den älteren Systematikern wurden indessen nicht nur Farbendifferenzen angegeben, sondern, jedenfalls für *phoenicea* und *coerulea*, auch andere unterscheidende Merkmale. Wie verhalten sich nun diese Eigenschaften in Kreuzungen?

Ich habe die S. 97 angegebenen Differenzen an mehreren Provenienzen der Formen untersucht. Hierbei hat sich herausgestellt, dass die betreffenden Eigenschaften durchweg keine charakteristischen Merkmale der Formen sind, sondern ganz unabhängig von der Farbe variieren, also *als Artmerkmale rein fiktiv sind.* Auch die in floristischen Arbeiten immer neben der Blütenfarbe als essentiell angesehene Eigenschaft der Bewimperung des Randes der Blütenkrone ist nicht haltbar.

Schon HARTMAN hat in seiner Flora, V. Aufl. (1849) hervorgehoben, dass die Kronenblätter bei *β coerulea* ebenso stark bewimpert sind wie bei der rotblütigen Hauptart. Ebensowenig stimmen die anderen oben (S. 97) angeführten Merkmalsdifferenzen. Hierdurch ist klar, dass *phoenicea* und *coerulea ganz und gar Farbenformen sind*, ebenso wie man dies für *carnea* allgemein angenommen hat. *Alle drei Formen sind indessen ganz gleichwertig*, und es ist nicht richtig, *carnea* unter *phoenicea* oder *coerulea* als eine Form niedrigeren Ranges unterzuordnen. Als Subspezies werden die letzteren von LÜDI (bei HEGI) angeführt, während *carnea* nur als forma zu *phoenicea* gestellt wird. Da man indessen für Subspezies mehr als eine einzige unterscheidende Eigenschaft annehmen muss, ist diese Bezeichnung nicht geeignet. LÜDI führt zwar einige neue Unterschiede an in bezug auf die Anzahl von Zellen der Haare am Rande der Petalen und der Staubfädenhaare. Sie scheinen aber ebenso fraglich zu sein wie die übrigen angegebenen differenten Merkmale, d. h., sie können stimmen oder nicht, ganz abhängig von den zufällig ausgewählten Individuen. Sie stimmen aber *nicht immer*, sondern die betreffende Variabilität ist innerhalb der Farbenformen zu konstatieren. Durchschnittlich sind die *coerulea*-Pflanzen wohl kräftiger als die *phoenicea*-Individuen, und erstere haben oft dunkler gefärbte Samen; hierauf aber Diagnosen zu bauen erscheint unmöglich.

Als Subspezies kann man wohl nicht eine Variante betrachten, die keine ökologische Differenzierung zeigt. Sowohl *phoenicea* als *coerulea* scheinen beide Ubiquisten ausserhalb der Tropen zu sein, nur ist erstere unvergleichlich häufiger. Auch *carnea* ist unter den anderen Formen sicher sehr verbreitet, nur ist sie noch seltener als *coerulea*. In Schonen (südlichstes Schweden) ist *carnea* von mir in Hörte, Gottorp und Bjerred gefunden. An sämtlichen Orten oder in deren unmittelbarer Nähe ist auch *coerulea* gefunden.

Als Subspezies können die *Anagallis*-Varianten also auch nicht betrachtet werden. Eine richtige Auffassung ihrer systematischen Natur hat gewiss POLLICH (vgl. oben p. 99), der sie sämtlich als *gleichwertige Farbenformen* anführt (*α*, *β* und c.). Er wäre also als Autor zu nennen, gibt aber kein Nomen varietatis, sondern nur Diagnosen. Ihm folgt WILLDENOW in Spec. plant., ed. IV. Gewöhnlich werden als Autoren, falls *phoenicea* und *coerulea* als Varietäten betrachtet werden, GRENIER et GODRON (1850) genannt. Aber schon BAUMGARTEN hat sie in seiner Flora lipsiensis (1790, p. 110—111) als Varietäten von *A. arvensis* L. angeführt. Die rosafarbige Variante wird in den Floren meistens nur als Farbenabweichung von Rot ohne jede Bezeichnung erwähnt. Zu-

weilen geht sie unter dem Namen *A. arvensis* f. *lilacina* ALEFELD. HOFFMANN betrachtet die beiden Formen als identisch (1879, p. 181). LÜDI führt die rosafarbige (fleischfarbige) Variante als f. *carnea* unter ssp. *phoenicea* auf.

Für die blaue Form habe ich bis hierher den Namen *A. coerulea* SCHREB. (1771) benutzt, weil dieser der allgemein bekannte und verwendete ist (vgl. ENGLER, KOCH und HEGI, l. c.). Dieser Name gibt ja auch die Variabilitätsrichtung der Form an. Er ist indessen nicht der älteste, sondern dieser ist *A. femina* MILLER (1768), von ihm als Speziesnamen verwendet. Als Varietätsnamen wird dieser zuerst von SCHINZ et THELLUNG (1907) benutzt.

Da die Farbenvarianten von *A. arvensis* L. in sämtlichen Kreuzungsverbindungen monohybrid spalten, müssen sie vom genischen Gesichtspunkt als multiple Allelomorphen betrachtet werden. Das besagt, dass sie nur Abstufungen ein und derselben erblichen Eigenschaft sind. Sie sind also, erblich gesehen, so kleine Varianten, wie man überhaupt finden kann. Dann müssen sie auch floristisch danach bezeichnet werden. Die hier behandelten Varianten von *Anagallis arvensis* L. sollen demnach folgende Bezeichnungen erhalten:

f. *phoenicea* (SCOP.) BAUMG.
f. *femina* (MILL.) SCHINZ et THELL.
f. *carnea* (SCHRANK) LÜDI.

Das Schicksal dieser *Anagallis*-Formen ist für die Speziesfrage sehr lehrreich. Es zeigt, wie Varianten einer Spezies, die erblich, also konstitutionell, extrem geringe Verschiedenheiten aufweisen, wegen eines auffallenden morphologischen Effekts, der in ungewöhnlicher Richtung geht, einen hohen systematischen Wert erhalten, als Spezies betrachtet werden. Weissblütige Formen würde es wohl niemand einfallen als Arten zu betrachten. Die Variation von Rot zu Blau bei einer wildwachsenden Art ist ungewöhnlich. Zwar haben wir bei *Anagallis* die rosablütige Form, die morphologisch den Übergang vermittelt, aber diese wollte man als Bastard betrachten. Der wirkliche Bastard ist aber morphologisch nicht sichtbar, und dies verwickelte das Problem noch mehr und hinderte eine richtige Auffassung. Nur der experimentellen Systematik ist es überhaupt möglich gewesen, die Frage zu lösen.

ZITIERTE LITERATUR.

1. BAUMGARTEN, J. 1790. Flora lipsiensis. — Leipzig.
2. DÖRFLER, I. 1903. Über den Bastard *Anagallis arvensis* × *coerulea*. — Verhandl. d. zool.-bot. Gesellsch. in Wien 53, p. 563—564.
3. ENGLER, A. 1905. Das Pflanzenreich. IV. 237. *Primulaceæ*. — Leipzig.
4. FOCKE, W. 1881. Pflanzenmischlinge. — Berlin.
5. GRENIER, M. et GODRON, M. 1850. Flore de France. Teil II. — Paris et Besançon.
6. GÄRTNER, C. F. v. 1849. Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich. — Stuttgart.
7. HARTMAN, C. 1849. Skandinaviens Flora. Ed. V. — Stockholm.
8. HEGI, G. 1926. Illustrierte Flora von Mitteleuropa, Bd. V, Teil. 3. — München.
9. HOFFMANN, H. 1879. Culturversuche. — Bot. Zeitung 37, p. 177—181.
10. — 1887. Culturversuche über Variation. — Ibid. 45, p. 24—27.
11. KOCH, W. D. J. 1907. Synopsis der Deutschen und Schweizer Flora. Ed. III, Bd. 3. — Leipzig.
12. LANGE, J. 1860. Pugillus plantarum, imprimis hispanicarum, quas in itinere 1851—1852 legit. — Hafniæ 1860—1861 (Naturhistorisk Forenings Meddelelser).
13. LINNÆUS, C. 1753. Species plantarum. — Holmiæ.
14. MILLER, PH. 1768. The gardeners and florists dictionary. Ed. VIII.
15. NILSSON, HERIBERT. 1912. Ärftlighetsförsök med blomfärgen hos *Anagallis arvensis* (Erblichkeitsversuche mit der Blütenfarbe der *A. arvensis*). — Bot. Notiser, p. 229—235.
16. POLLICH, J. A. 1776. Historia plantarum. Tomus prim. — Manhemii.
17. RUNDKWIST, E. 1914. Iakttagelser över två hybrider i Blekinge (Beobachtungen zweier Hybriden in B.). — Bot. Notiser, p. 127—129.
18. SCHINZ, H. und THELLUNG, A. 1907. Begründung vorzunehmender Namensänderungen in der zweiten Auflage der »Flora der Schweiz» von SCHINZ und KELLER. — Mitteil. aus dem Bot. Museum der Univ. Zürich 34.
19. SCHRANK, F. 1789. Baiersche Flora. Bd. I. — München.
20. SCHREBER, J. v. 1771. Spicilegium floræ lipsiæ. — Lipsiæ.
21. WEISS, F. E. 1911. Researches on heredity in plants. — Mem. Lit. Phil. Soc., Manchester, 56, pp. 1—12.
22. WILLDENOW, C. L. 1797. CAROLI A LINNÉ Species plantarum, Ed. IV, Tom. I, Pars 4. — Berolini.
23. WILLKOMM, M. et LANGE, J. 1870. Prodromus floræ Hispanicæ, Vol. II. — Stuttgartiæ.

A CLOSELY LINKED GROUP OF DOMINANT MUTATIONS IN THE THIRD CHROMOSOME OF DROSOPHILA MELANOGASTER

BY *JEANNE COYNE MOSSIGE*

ANATOMICAL INSTITUTE, THE UNIVERSITY, OSLO, NORWAY

THE region around 40 in the third chromosome of *Drosophila melanogaster* presents an interesting problem. Five dominant mutations, all of them lethal when homozygous, are listed at 40,4. These are Dichaete (D), Lyra (Ly), Glued (Gl), Minute-h (Mh) and Minute-y (My). Dichaete is manifested by wings outstretched at right angles to the body, the alulae and the anterior dorso-central bristles are absent. Ly also causes the wings to stand out from the body more than in wild type but not to such an extent as in D. The wing margins are extremely ragged so that the total wing area is about cut in half. Glued affects the eyes only, reducing their size and producing irregular, run-together ommatidia. Mh and My are typical Minutes, reducing the size of the bristles and causing a delay in larval development. Except for the two later, this group does accordingly not present the picture of a typical allelomorphic series.

The occurrence of a new mutation, M33j, led to the experiments described below. M33j, a typical Minute, was induced by x-rays by M. DEMEREC. Preliminary tests to locate the new Minute showed it to be between h (26,5) and th (42,2) in the third chromosome. A cross was made of M33j to Ly/D with the intention of determining its relation to D but this proved to be unnecessary when the combination Ly/M33j was found to be lethal. In a total of 2415 offspring no Ly/M33j flies survived where 25 % were expected. This points to the possibility that M33j is a section deficiency including the Ly locus and immediately gave a definite starting point from which to investigate the order of the five dominant mutations already listed at this locus. All possible combinations of all six mutations were tried and except for the fact that any one of the three Minutes is lethal in combination with the other two, and the above mentioned Ly/M33j combination, none of the others proved to be lethal. The results of these viability tests for those combinations which are lethal are presented in Table 1.

TABLE 1.

♀ ru jv se M33j/Payne × ♂ se Mh H/LVM

Payne/LVM	ru jv se M33j/LVM	se Mh H/Payne	ru jv se M33j/se mh H	Total
969	690	647	0	2306

♀ Mh/D × ♂ My/Ly

Ly/D	Ly/Mh	D/My	Mh/My	Total
377	322	58	0	757

♀ Ly/Mh × ♂ D/My

Ly/D	Ly/My	D/Mh	My/Mh	Total
72	54	45	0	171

♀ ru jv se M33j/Payne × ♂ ru jv se My/Payne

M (undistinguishable but non-ru jv se)
1252

♀ Ly/D × ♂ M33j/Payne

Ly/Payne	D/Payne	D/M33j	Ly/M33j	Total
905	840	670	0	2415

SCHULTZ (1929) has shown in extensive experiments that Minutes do not have a cumulative effect, but that any two non-allelomorphic Minute mutations when present in a single individual, present the characteristics of the most extreme Minute of the two present. Therefore the lethal results of the combinations of the Minutes in the present case, justify the opinion that they may all three be section deficiencies partly overlapping, and not merely the result of a cumulative lethal effect. According to this method of reasoning M33j must be overlapping, though not identical with Mh and My as demonstrated by the lethality of the M33j/Ly combination while Mh and My survive in combination with Ly. We know that many but not all Minutes are section deficiencies. As demonstrated by BRIDGES (MORGAN, BRIDGES and SCHULTZ, 1933) in the case of Ml and Ml^2 these two are lethal in combination and yet both genetic tests and examination of salivary gland chromosomes show that Ml is a section deficiency while Ml^2 is not.

Although the possibility of allelomorphism is practically ruled out except for Mh and My it is interesting to note some of the similarities of the phenotypic effects of the various mutations in question. Frequently both My and M33j flies have wings with ragged edges, similar to, but not as extreme as Lyra. All the Minutes, not only the three

under discussion, have a tendency to produce slightly roughened eyes with irregular ommatidia. But this in no way approaches the effect produced by the Glued mutation. The combination My/D is of very low viability and results in flies with wide set, bulging eyes, irregular facets, ocelli and ocellar bristles frequently lacking, and all thoracic bristles greatly reduced in size and irregularly directed beyond the independent effects of either My or D alone. The wings are frequently puffy, of the balloon type, with extreme plexate venation. The thorax is often asymmetrical. These effects are very extreme but such effects are also produced by combinations of genes located in different chromosomes, so this can hardly be considered as evidence that My is a deficiency for or an allel of D, a possibility which is definitely eliminated by the linkage tests to be presented below. All three of the Minutes in combination with Ly, D and Gl tend to produce irregularities similar to, though not as extreme as those described above, and reduce viability and fertility to such an extent as to make linkage experiments difficult and more or less unreliable because of the small number of offspring produced. In almost all cases it was necessary to use several pairs in each bottle. A preliminary report on these linkage tests before their completion appeared in D. I. S. IV (COYNE, 1935). Crossover tests were made between all viable combinations of five of the mutations with the exception of Ly and Gl as PLOUGH's evidence shows no crossing over between these two mutations in 5000 test flies (PLOUGH and IVES, 1935). My was not tested on the assumption that it is identical for these purposes, with Mh.

LINKAGE TESTS.

1. The Ly/Gl female test cross.

se Gl/Ly × seple

se Gl	Ly	Gl	se Ly	se	Gl Ly	Total
707	700	106	110	9	1	1633

This gives a total of 10 recombinations for Gl and Ly out of 1633 flies, corresponding to a map distance of 0,6 units proving that Ly and Gl are not allels. The marker sepia shows that Ly lies to the left of Gl.

2. The Mh/Gl female test cross.

Gl/se Mh H × seple

Gl	se Mh H	se Gl	Mh H	se Mh	Gl H	se Gl H	Mh	H	se Mh Gl	se Mh Gl H	+	Total
411	384	68	42	55	68	7	6	3	1	7	4	1056

This gives 15 recombinations for Mh and Gl in a total of 1056 flies corresponding to a crossover percentage of 1,4. The phenotypes of the crossover classes indicate that Mh lies to the left of Gl.

Since we know that M33j is lethal in combination with Ly and also with Mh and My, while Mh and My do not extend as far to the right as Ly, this would place M33j to the left of and including Ly, while overlapping part or all of the Mh—My region.

3. The Mh/Ly female test cross.

Ly/se Mh × seple

Ly	se Mh	se Ly	Mh	se Mh Ly	Total
627	545	94	69	2	1337

In this case the 2 crossovers between Ly and Mh represent a map distance of 0,15. This confirms the fact that Ly lies to the left of Gl and demonstrates that Ly and Mh are not allels.

4. The Mh/D female test cross.

a) D/se Mh × seple

D	se Mh	se D	Mh	Total
221	186	42	35	484

b) D/se Mh H × seple

D	se Mh H	se D	Mh H	se Mh	D H	se D H	Mh	se D Mh	se Mh D H	Total
431	307	82	52	67	111	5	1	1	2	1059

The three recombinations in a total of 1543 (a + b) correspond to 0,2 % crossing over. This is just barely greater than the Mh—Ly distance and confirms the fact that Mh and D are not allels as well as suggesting that Ly lies to the left of D, and this latter circumstance is confirmed by the fact that M33j includes Ly but does not extend far enough to the right to include D also.

5. The M33j/Gl female test cross.

a) se Gl/M33j × seple

se Gl	M33j	Gl	se M33j	Total
382	309	40	41	772

b) ru jv se M33j × seple

se M33j	Gl	se Gl	M33j	Total
59	82	13	13	167

6. The M33j female test cross.

a) se D/M33j × ru jv se

se D	M33j	D	se M33j	Total
114	151	14	19	298

b) ru jv se M33j/D × seple

se M33j	D	M33j	se D	Total
143	228	24	43	438

7. The Ly/D female test cross.

Ly/D × M33j/Payne

Ly	D	D/M33j	Total
905	840	670	2415

The fact that there is no crossing over between Ly and D is reasonable in view of their proximity. It may also be added, that in addition to the test cross number 7, Ly/D has been maintained in the laboratory as a balanced stock for several years and no crossovers have been detected. However that there is no crossing over between D and Gl, in a distance of 1,2 units (this distance calculated by subtracting Mh—D from Mh—Gl distances) is unexpected. The fact that M33j, which obviously extends to the left of Ly since it is lethal in combination with Mh and My, gave no crossing over with D or with Gl, may be explained by assuming that M33j as well as possibly D, reduce or prevent crossing over in their immediate neighbourhood.

Using D as the 40,4 locus, Ly would be at 40,4 — and Mh at 40,2. The Mh—Gl data place Gl at 41,6 (40,2 + 1,4) while the Ly—Gl crossover data confirm this well if the crossover distance 1,1 for 822 flies (based on non-Ly flies only) is added to Ly at 40,4 —. Using the total data in the Ly—Gl test this distance is reduced to 0,6 and since the Mh—Ly distance equals 0,15 this would make the total distance between Mh and Gl 0,75 whereas the distance by direct test is 1,4. Since previous experience has shown that the combination Gl/Ly is of low viability and since the test cross se Gl/Ly × seple (No. 1) gives equal reciprocal classes in all cases except the crossovers of region 2 where 9 of the 10 flies are se and only 1 Gl Ly, it seems more reasonable to base the calculations on the non-Gl (or non-Ly) flies only than on the total. Thus it follows that the measurements by direct test are probably more reliable in this case than reduced measurements derived from weighted values on a basis of this single Gl—Ly cross. This procedure seems

especially justified in view of the short distances involved. A map of the region, based on the face value of these experiments is presented in Fig. 1.

Fig. 1. This map roughly indicates the relationship of the six dominants involved. The exact points at which M33j and Mh and My (if the two later are deficiencies) begin and end is undetermined except in so far as M33j extends to the right to a point between Ly and D.

An attempt was made to induce crossing over between Ly and D by using inversions in the first and second chromosomes in the Ly/D linkage tests. This method used by STEINBERG (1936) and others, has been found to increase crossing over in the first chromosome when inversions were present in the second and third. The cross was made as follows:

♀ Cl B/+; Ly/+; Ly/se D × ♂ seple

Ly	se D	se Ly	D	Total
790	827	238	220	2075

In the present case the inversions in the first and third chromosomes failed to induce crossing over between Ly and D while the crossover percentage between se and D is very markedly increased. The distance between se and D is 14,4 while in this particular cross it is 22. No controls were run but in all the other linkage tests reported in this paper the distance from se to all of the dominants in the group was very close to the standard map distance. Sepia was used as a marker in these tests because it happened to be convenient in the stocks but it is too far to the left to be useful as a point from which to measure crossovers with genes at the 40,4 locus where such small distances are involved.

A striking feature of the linkage tests are the phenotypes of the crossovers between D—Mh and Ly—Mh. It would seem much more likely that crossovers of the + type should survive but this was not the case. This result is so far unexplained.

Two other mutations located near the 40,4 locus have also been tested. Tilt (tt listed at 40,2) proved to be slightly to the left of Mh. Crimp (Cm, at 39 —) was tested for viability with all six of the dominants and all combinations were viable. The difficulty of classi-

fying Cm in combination with the Minutes and with Ly made cross-over experiments impractical. Unpublished data of Prof. O. L. MOHR indicate that Cm probably lies to the right of the group of dominants under discussion.

Examinations of salivary gland preparations will be necessary to complete the study of this group of mutations and should yield practical results if M33j proves to be a section deficiency including the Ly locus.

In summing up the results of these tests it appears that six dominant lethal genes, listed at 40,4 in the third chromosome cover a map distance of 1,4 units from 40,2 to 41,6, using D as the 40,4 locus. The order of these genes from left to right is Mh = My, M33j (overlapping both Mh—My and Ly), Ly, D, Gl.

Acknowledgements. — I would like to express my thanks and appreciation to Prof. O. L. MOHR, Anatomical Institute, The University, Oslo, and to Prof. L. C. DUNN, Columbia University, New York, for their advice and criticism in the present work.

LITERATURE CITED.

1. COYNE, J. 1935. Crossing over within a closely linked group of genes near locus 40,4 of chromosome 3. — »Drosophila Information Service», 4: 59.
2. MORGAN, T. H., BRIDGES, C. B. and SCHULTZ, J. 1933—34. Report on investigations on the constitution of the germinal material in relation to heredity. — Carn. Inst. Wash. Yearbook, No. 33: 274—280.
3. PLOUGH, H. H. and IVES, P. T. 1935. Induction of mutations by high temperature in *Drosophila*. — Genetics, 20: 42—69.
4. SCHULTZ, J. 1929. The Minute reaction in the development of *Drosophila melanogaster*. — Genetics, 14: 366—419.
5. STEINBERG, A. G. 1936. The effect of autosomal inversions on crossing over in the X chromosome of *Drosophila melanogaster*. — Genetics, 21: 615—624.

STERILITY AND CHROMOSOME PAIRING IN INTRASPECIFIC GALEOPSIS HYBRIDS

BY *ARNE MÜNTZING*
SVALÖF, SWEDEN

I. INTRODUCTION.

As demonstrated in previous papers concerning the genetics of the genus *Galeopsis* (MÜNTZING, 1929, 1930 a and b, 1932 a and b, 1937 a), most of the species in this genus are autogamous and thus composed of pure lines. These lines have an excellent fertility on the male as well as on the female side. The percentage of apparently good pollen grains almost always amounts to at least 90 per cent and generally lies between 95 and 100. Pollen fertility and its variation has been especially studied in the tetraploid species, *G. Tetrahit*. In this species crosses between different pure lines often give F_1 generations with a markedly reduced fertility. Consequently, *G. Tetrahit* is characterized by the occurrence of intraspecific sterility, which is met with in certain definite line combinations. Many F_1 combinations, however, have the same or approximately the same good fertility as the parent lines, but in other cases about half or a quarter of the pollen is bad and also the seed production is reduced.

The previous investigations concerning the nature and inheritance of this intraspecific sterility gave the following main results (MÜNTZING, 1929, 1930 a, 1932 a):

1) The sterility is selective and is caused by the lethality of definite categories of recombination gametes.

2) In some crosses at least sterility is inherited in a rather uncomplicated way, which is possible to analyse genetically. — In the simplest cases the partial sterility depends on a bifactorial (or bistructural) difference between the lines crossed, and in such a case either both or only one of the two types of recombination gametes are lethal. This lethality is more pronounced in the pollen than in the ovules.

3) Lines which are fertile with each other often behave in the same way when crossed to other lines. For that reason it is possible, to a certain extent, to distinguish intrafertile but intersterile groups of lines.

The preliminary group delimitation reported in the paper 1930 a (p. 231) was based on 24 different crosses, involving 8 pure lines. Since that was written many new crosses have been made. During this work the main idea was to cross a limited number of lines in all possible directions. For that purpose 12 different lines were selected, and these have now been combined in all the 66 combinations possible $\left(\frac{n^2-n}{2}; n = 12\right)$.

The present paper represents an analysis of the different degrees of fertility in these 66 kinds of F_1 hybrids. Further new cytological results have been obtained, which are considered in relation to the sterility phenomena met with.

II. POLLEN FERTILITY IN PURE LINES AND F_1 COMBINATIONS IN GALEOPSIS TETRAHIT.

1. PURE LINES.

The pure lines, used for the crosses, are partly those involved in the preliminary group delimitation (1930 a, p. 231), *viz.* *T—A*, *T—B*, *T—C*, *T—D*, *T—E*, *T—F*, *T—G* and *T—X*, but in addition to these lines four new biotypes (*T—I*, *T—J*, *T—L* and *T—M* [1]) enter into the crosses.

Nine of these 12 lines are of Swedish origin (8 collected in the Province of Skåne, 1 in Gothenburg), while the remaining three (*A*, *C* and *M*) were obtained from the Botanical Gardens of Tabor, Riga and Eastborne. Most of the lines have been in culture since 1925, and all of them have been constant from the beginning. The morphological differences between the lines are rather marked and affect all kinds of vegetative as well as floral characters (cf. MÜNTZING, 1930 a, Figs. 4—8, p. 232 and Pl. IV). There are also considerable line differences with respect to such physiological characters as earliness and germination energy.

As already pointed out in the introduction, these homozygous lines are characterized by excellent fertility (cf. Fig. 28, p. 166). Every year, parallel with the investigations of the F_1 generations, pollen fertility has been examined in all or part of the parent lines. Concerning pollen fertility in the pure lines all data obtained have been summarized in Table 1. In addition to the twelve lines mentioned above, this table also includes three additional lines (*T—N*, »glabra» and »yellow

[1] For the sake of brevity, these lines will be designated in the following pages by *A*, *B*, *C*, etc. instead of *T—A*, *T—B*, *T—C*, etc.

Tetrahit») not involved in the series of diallel crosses. The lines have been studied for several years (on an average 6—7 years), and in each year polien samples from 3 to 10 plants were examined. The total number of plants examined in the different lines varies between 10 and 64. The methods used for the determination of the percentage of good pollen have been described in previous papers.

TABLE 1. *Pollen fertility in pure lines of G. Tetrahit.*

Line	Number of years when investigated	Percentage of good pollen: 60	65	70	75	80	85	90	95	100	Number of plants	M
A	8								12	31	43	96,1
B	9							1	3	43	47	97,0
C	9			1	—	—	1	4	10	48	64	95,4
D	9					1	1	—	3	43	48	96,5
E	7						1	—	1	43	45	97,1
F	8			1	1	—	—	1	5	35	43	95,4
G	6		1	—	—	1	2	5	11	21	41	92,9
I	5				1	—	1	2	7	12	23	93,4
J	5						1	6	6	9	22	92,7
L	5		1	—	—	1	2	2	2	14	22	92,3
M.....	6						1	—	3	25	29	96,5
N.....	5								1	30	31	97,3
X.....	6			1	—	—	—	1	9	28	39	95,3
»*yellow Tetrahit*»	5			1	1	—	1	3	10	15	31	92,7
»*glabra*»...	2								1	9	10	97,0

As is evident from the table, the maximum class in all the lines lies between 95 and 100, and the average values vary between 92,3 and 97,3. It is true that single plants, probably due to occasional external disturbances, have given pollen samples with a more or less high percentage of bad pollen. On an average, however, the pure lines investigated are characterized by an excellent pollen fertility.

2. F_1 COMBINATIONS.

A. FREQUENCY AND DEGREE OF PARTIAL STERILITY.

All data on pollen fertility in the 66 F_1 combinations have been concentrated to the following scheme (Diagram 1). In this diagram the total average value of each combination (the percentage of apparently good pollen) is given and, in brackets, the number of individuals on which this average is based. From lack of space it has not been possible to represent the 66 different distributions, but only their average values. In previous papers, however, several examples of such distributions

have been given (MÜNTZING, 1929, p. 309, and 1930 a, p. 229). Since the new series, obtained later, were found to be of quite the same type, it does not seem necessary to give any more details of this kind.

In most cases the crosses were performed in both the possible

DIAGRAM 1. *Pollen fertility in 66 F_1 combinations between 12 pure lines of Galeopsis Tetrahit.*
(The number of individuals in brackets.)

	X	M	L	J	I	G	F	E	D	C	B
A	71 (28)	96 (6)	94 (5)	79 (12)	70 (17)	93 (11)	78 (4)	95 (6)	94 (9)	74 (5)	97 (5)
B	54 (64)	97 (12)	97 (8)	84 (10)	50 (9)	87 (36)	64 (9)	76 (21)	98 (14)	57 (82)	
C	94 (15)	54 (26)	58 (5)	94 (11)	67 (9)	89 (18)	96 (15)	94 (12)	79 (10)		
D	95 (11)	94 (32)	69 (5)	93 (12)	73 (18)	89 (12)	96 (5)	93 (10)			
E	94 (25)	79 (6)	69 (11)	98 (3)	68 (8)	88 (20)	93 (6)				
F	98 (14)	61 (6)	64 (11)	98 (2)	63 (7)	92 (4)					
G	95 (12)	90 (15)	90 (7)	90 (6)	75 (4)						
I	72 (8)	56 (5)	69 (11)	56 (14)							
J	98 (3)	75 (21)	69 (3)								
L	56 (13)	98 (2)									
M	51 (7)										

directions. The percentage values of the F_1 plants were always found to be independent of the direction of the cross, and no significant differences were observed between the fertility of the two reciprocal combinations. This being the case, a common average value has been calculated for each cross combination, without considering the direction of the cross.

In many cases the same F_1 combination was examined in two or more years. This was possible only by repeating the crosses, the *Galeopsis* species all being annual. Apart from slight average changes, characteristic of different years and affecting all F_1 types grown this year in the same direction, the average values of a certain combination were found to be very much similar in different years. Therefore a common average value has been calculated from the values obtained in different years. This may be exemplified as follows:

The hybrids between the *B* and *C* lines were examined in eight different years, giving the average values 55, 53, 53, 58, 61, 69, 55 and 62 per cent respectively (cf. Fig. 29, p. 167). The number of F_1 plants in the different years varied between 1 and 21. — The cross $B \times X$ (and reciprocally) was made in five different years, the resulting F_1 plants having the following average values: 56, 61, 52, 56 and 54. In this cross the number of individuals in the different years was 2, 3, 13, 12 and 34 respectively.

A less severe degree of sterility than in the two preceding cases is characteristic of the hybrids between *A* and *X*, F_1 generations from four different years giving the values 76, 64, 69 and 71 per cent (6, 4, 5 and 13 plants examined). — The sterility is still weaker, *e. g.* in the hybrids between *B* and *G*, the values obtained in each of five years being 94, 89, 78, 85 and 90. These values are based on 3, 5, 2, 14 and 12 individuals respectively. The following two cases, finally, represent crosses giving fertile F_1 generations. In 1928 eight F_1 plants, representing the combination $E \times X$, had on an average 94 per cent good pollen. In 1931 the same combination gave the value 95 and in 1937 92 per cent (12 and 5 individuals respectively). The cross $D \times M$ gave exactly similar results. The average values obtained in 1931, 1933 and 1937 were 94, 93 and 95 per cent, these values being based on the examination of 5, 6 and 21 plants respectively.

In this way 23 of the 66 cross combinations possible have been examined more than once. As is evident from the examples given above, the values of different years agree with each other rather well. All other F_2 combinations, examined more than once, were found to behave in the same way. The differences between the values of different years are due to the limited number of individuals, the limited number of pollen grains observed from each plant and probably also to general environmental differences between the years.

In spite of these difficulties, however, it is quite obvious that *each F_1 combination is characterized by a certain typical degree of fertility.*

$B \times C$ hybrids are always markedly pollen sterile, just as $B \times X$, $C \times M$ and many other combinations. On the other hand, in the $A \times X$, $B \times E$ and $J \times M$ hybrids, for instance, only about a quarter of the pollen grains are shrivelled, and in other combinations again such as $B \times G$ the fertility reduction is very slight but nevertheless significant. Finally, several combinations are apparently quite fertile.

According to previous investigations (MÜNTZING, 1929, 1930 a), it seemed possible to divide the F_1 hybrids into the following three categories: a) fully fertile, b) semi-sterile (with about 50 per cent bad pollen) and c) quarter-sterile (with about 25 per cent bad pollen). If that is generally the case in *Galeopsis Tetrahit*, the 66 average values now obtained should be grouped in the same three categories. If these values are arranged in a series the following result is obtained:

Percentage of good pollen:	50—55	55—60	60—65	65—70	70—75	75—80	80—85	85—90	90—95	95—100
Average values of the F_1 combinations	4	5	4	6	5	7	1	4	15	15

The mean values of the F_1 combinations vary between 50 and 100, but there is evidently only one definite maximum, lying between 90 and 100. There is no trace of a limit between semi-sterile and quarter-sterile combinations, nor any discontinuity between F_1 generations which are as fertile as the parent lines and those showing a slight degree of sterility. Since, on an average, all pure lines examined under the same conditions had more than 90 per cent good pollen, it seems convenient, however, to fix the limit between fertile and partially sterile F_1 combinations at 90 per cent. Thus F_1 combinations with values below 90 will hereafter be counted as partially sterile. According to this delimitation 30 of the 66 combinations are to be regarded as fertile and no less than 36 as partially sterile. *Thus, in G. Tetrahit it frequently happens that the F_1 hybrids between different pure lines have less good fertility than the parent lines, but the degree of this sterility varies continuously within rather wide limits.*

Since it is rather remarkable that pure lines, belonging to one and the same species, so frequently give partially sterile F_1 hybrids, this might be suspected to depend on a few strongly deviating lines, the other lines being fertile with each other. This possibility has been tested in Table 2. In this table the percentage of good pollen is given for the 11 different F_1 combinations which each separate line gives with the other eleven lines. Thus, according to the table, the *A* line, for instance,

gives 6 fertile and 5 sterile [1] F_1 generations with the other lines, the average values of the sterile combinations all lying between 70 and 80. The *B* line gives 4 fertile and 7 sterile combinations, the pollen fertility of the latter varying between 50 and 90, etc.

As is evident from the table, *there are significant differences between the lines with regard to the frequency and degree of sterility in combination with the other lines.* The strongest contrast is shown by the lines *G* and *I*. The latter line is remarkable in that it gives sterile F_1 generations with all the other eleven lines. This sterility is in all the combinations quite distinctly evident, the percentage of good pollen ranging from 50 to 80. Line *G*, on the contrary, gives a much better

TABLE 2. *Average pollen fertility in the F_1 generations formed by each line in combination with the other 11 lines.*

Cross combination	Percentage of good pollen: 50	55	60	65	70	75	80	85	90	95	100	n	Number of sterile F_1 combinations
A × the other lines						3	2	—	—	3	3	11	5
B × »		2	1	1	—	—	1	1	1	—	4	»	7
C × »		1	2	—	1	1	1	—	1	3	1	»	7
D × »					1	1	1	—	1	4	3	»	4
E × »					2	—	2	—	1	4	2	»	5
F × »				4	—	—	1	—	—	2	4	»	5
G × »							1	—	4	5	1	»	5
I × »		1	2	1	3	3	1					»	11
J × »			1	—	1	—	2	1	—	3	3	»	5
L × »			2	1	4	—	—	—	—	2	2	»	7
M × »		2	1	1	—	—	2	—	—	2	3	»	6
X × »		2	1	—	—	2	—	—	—	2	4	»	5

fertility in crosses with the other lines. Six of the F_1 generations have at least 90 per cent good pollen and may thus be regarded as fully fertile. The other 5 combinations are partially sterile, it is true, but 4 of them have a pollen percentage amounting to between 85 and 90.

The other lines are less extreme, all of them giving rise to fertile as well as sterile F_1 generations in about equal numbers. Thus, on an average, the table strongly indicates that *the causes leading to sterility in the F_1 generations are distributed among all the lines and not only characteristic of a few of them.* The particular position of the *I* line has been emphasized, it is true, but this line can only be responsible for 11 of the 36 sterile combinations at most.

[1] Here and in the following pages »partially sterile» is abbreviated to »sterile».

B. GROUP DELIMITATION.

As already mentioned in the introduction, it has been possible to a certain extent to distinguish groups of intrafertile but intersterile lines. In my paper of 1930 a (p. 231) 5 such groups are represented, which are based on 24 combinations between 8 lines. In order to test the possibility of such a group delimitation in the present, more extensive material, the following procedure was employed: *If two lines are to be included in the same group they must not only be fertile with each other but also react in the same way with all the other ten lines.* Thus, in order to find out how the lines behave in this respect and to get a general measure of the genotypical similarity, with respect to causes of sterility, it is necessary to combine the lines two by two in the 66 directions possible and to examine to what extent the lines behave similarly or differently when crossed to the other lines. This examination gave the following result (Table 3):

Among the 30 fertile combinations there are only three in which both the lines react in the same way with all the other lines. These line pairs are *F* and *J*, *F* and *X* and *X* and *J*. Thus, the lines *F*, *J* and *X* are not only fertile *inter se* in all directions but they also react in exactly the same way with the other nine lines. *F* and *J*, as well as *X*, give fertile F_1 generations with the lines *C*, *D*, *E* and *G* and sterile F_1 generations with *A*, *B*, *I*, *L* and *M* (cf. Diagram 1).

The other fertile combinations involve line pairs, behaving more or less differently with regard to the remaining lines. Under such circumstances the members of the line pairs cannot belong to the same group, as they are evidently different with regard to the causes of sterility. However, the similarity in behaviour is sometimes very great. This is true especially of the lines *B* and *M*, which are fertile with each other, and further demonstrate their similar constitution by reacting in the same way with nine of the other lines (fertile with *A*, *D* and *L*, sterile with *C*, *E*, *F*, *I* and *J*) and differently only as regards the line *G*. This difference, however, is more likely to be formal than real. The cross $B \times G$ gave F_1 plants with an average of 87 per cent good pollen, the corresponding value of the cross $M \times G$ being 90 per cent. The difference in fertility is only 3 per cent, but since the limit between fertile and sterile combinations lies just at 90 per cent, the former F_1 combination must be counted as sterile, the latter as fertile. At any rate the constitutions of *B* and *M* are very much similar with respect to the causes of sterility in crosses with other lines. Whether the lines

are quite identical or slightly different in this respect, can only be decided by further investigations. Provisionally, however, they must be considered to belong to different groups.

TABLE 3. *Survey of the mode of reaction of the 66 line pairs in crosses with the other 10 lines.*

	Line pairs	Number of combinations in which the lines compared behave		Line pairs	Number of combinations in which the lines compared behave	
		a) in the same way	b) differently		a) in the same way	b) differently
The lines compared are fertile with each other	A and B	8	2	D and J	5	5
	A » D	5	5	D » M	4	6
	A » E	2	8	D » X	5	5
	A » G	4	6	E » F	8	2
	A » L	8	2	E » J	8	2
	A » M	9	1	E » X	8	2
	B » D	5	5	F » G	4	6
	B » L	8	2	F » J	10	0
	B » M	9	1	F » X	10	0
	C » E	8	2	G » J	4	6
	C » F	8	2	G » L	6	4
	C » J	8	2	G » M	5	5
	C » X	8	2	G » X	4	6
	D » E	7	3	J » X	10	0
	D » F	5	5	L » M	9	1
The lines compared are sterile with each other	A and C	2	8	D and I	3	7
	A » F	4	6	D » L	5	5
	A » I	4	6	E » G	6	4
	A » J	4	6	E » I	4	6
	A » X	4	6	E » L	2	8
	B » C	2	8	E » M	3	7
	B » E	4	6	F » I	4	6
	B » F	2	8	F » L	2	8
	B » G	5	5	F » M	3	7
	B » I	6	4	G » I	4	6
	B » J	2	8	I » J	4	6
	B » X	2	8	I » L	6	4
	C » D	7	3	I » M	5	5
	C » G	6	4	I » X	4	6
	C » I	6	4	J » L	2	8
	C » L	2	8	J » M	3	7
	C » M	1	9	L » X	2	8
	D » G	7	3	M » X	3	7

Two additional fertile combinations, *A* and *M* and *L* and *M*, react in the same way with nine of the other lines and differently only in one case. *A* and *M* are both fertile with the lines *B*, *D*, *G* and *L* and sterile with *C*, *F*, *I*, *J* and *X*. *A* and *M* react differently only with regard to line *E*. The cross $A \times E$ gave the value 95 per cent, while $M \times E$

resulted in sterile F_1 plants with an average of 79 per cent good pollen. This difference is probably not accidental but is the expression of a constitutional dissimilarity between *A* and *M*. — The same thing holds good of *L* and *M*, these lines being fertile with *A*, *B* and *G* and sterile with *C*, *E*, *F*, *I*, *J* and *X*. With regard to the line *D*, however, *L* and *M* behave differently, $L \times D$ giving the value 69 per cent, whereas the $M \times D$ plants had an average of 94 per cent good pollen.

In 10 of the 30 fertile combinations the line pairs behave in the same way with 8 of the other lines but react differently with 2 lines. As is evident from Table 3, that is the case with regard to the following line pairs: *A*—*B*, *A*—*L*, *B*—*L*, *C*—*E*, *C*—*F*, *C*—*J*, *C*—*X*, *E*—*F*, *E*—*J* and *E*—*X*. Evidently the members of these pairs are rather similar, with respect to the causes of sterility, but they nevertheless present clear differences. — It is of interest that these line pairs may be grouped in the following way:

The lines *C* and *E* are not only relatively closely related but are also quite similar in constitution to the group of lines, *F*, *J* and *X*, discussed above. As already mentioned, *C* and *E* react in the same way in 8 and differently in 2 cases. The same thing also holds true of these two lines in combination with all members of the *F*—*J*—*X* group, i. e. as regards the pairs *C*—*F*, *C*—*J*, *C*—*X* as well as *E*—*F*, *E*—*J*, *E*—*X*.

A similar relatively close constitutional similarity is present between the lines *A*, *B*, *L* and *M*. As mentioned above, the combinations *A*—*M*, *B*—*M* and *L*—*M* react equally in 9 cases out of 10, the members of each pair thus reacting differently only with one of the ten other lines. An interesting feature is that the three remaining possible combinations between *A*, *B*, *L* and *M* behave in a somewhat similar way. Thus, a comparison between *A* and *B* shows that these lines react in the same way in 8 cases out of 10 and exactly the same thing is true of the combinations *A*—*L* and *B*—*L*. Thus, though not quite identical with regard to the causes of sterility, the lines *A*, *B*, *L* and *M*, nevertheless, form a rather closed group. The average constitution of this group is markedly different from that of the other group discussed above (*F*, *J*, *X*, *C* and *E*). Of the 20 cross combinations possible between these groups (consisting of *A*, *B*, *L*, *M* and *F*, *J*, *X*, *C*, *E* respectively) as many as 19 result in sterile F_1 generations, only one combination ($A \times E$) being fertile.

The three lines, *D*, *G* and *I*, not entering into any of the two groups just discussed, are also quite different *inter se*. Thus, *D* and *G* are sterile with each other and react differently in 3 cases out of 10. *D* and *I* are

also sterile with each other and react differently in 7 cases out of 10. *G* and *I*, finally, are also sterile with each other (as in all *I*-crosses) and react differently in 6 cases out of 10.

The lines *D*, *G* and *I* are not only different *inter se* but also quite different from the two groups, comprising the remaining 9 lines. The greatest similarity in this case is between *D* and *E*, these lines being fertile with each other and reacting in the same way with the other lines in 7 cases out of 10. All the other combinations between *D*, *G*, *I* and the two groups represent higher degrees of dissimilarity (cf. Table 3).

From the data given above it is evident that only three of the twelve lines tested, *viz*. *F*, *J* and *X*, behave in exactly the same way in crosses with other lines. Then since these lines are also fertile with each other, there is good reason to consider their constitution as identical or very much similar as regards the causes of sterility or fertility. It is possible that further crosses with new lines will reveal differences in reaction, the *F* line, for instance, giving fertile hybrids with a certain line, while *J* or *X* may react in the opposite way. Provisionally, however, *F*, *J* and *X* may be regarded as isogeneous (and structurally identical) with regard to the causes of sterility.

As already emphasized, all the remaining lines are different *inter se* and different from the *F*—*J*—*X* group. *Thus in regard to the causes of sterility, the twelve lines tested represent not less than ten different types.* It is possible, of course, that this number may be lowered to nine, the observed difference in reaction between *B* and *M* being very slight and perhaps not significant. In any case the number of »sterility types» is surprisingly high.

If only the *relative* similarity between the lines is taken into consideration, it will be found, as demonstrated above in detail, that the lines fall into two groups (*F*, *J*, *X*, *C*, *E* and *A*, *B*, *L*, *M*) and three independent lines, *D*, *G* and *I*.

C. CORRELATION BETWEEN GROUP DELIMITATION, MORPHOLOGY AND GEOGRAPHICAL ORIGIN.

It may be of interest to examine the possible occurrence of a correlation between morphology and geographical distribution, on the one hand, and the group delimitation, based on the sterility reactions, on the other. — Firstly, it is evident that the morphological characters have nothing to do with the sterility groups. All the twelve lines involved are different in flower colour as well as in vegetative characters. Of the lines in the first group (*F*, *J*, *X*, *C* and *E*) *F*, *J* and *E* are red-

flowered with different intensity and colour distribution, the *X* line being dominant white and *C* recessive white (cf. MÜNTZING, 1930 a, 1937 a). These lines also differ considerably in their vegetative characters. The only properties these lines have in common are earliness and a relatively low height, these characters being especially typical of *J* and *X*. It is probable, however, that these similarities are accidental and of no great significance. — The lines in the other group, *A*, *B*, *L*, *M*, are also very different in vegetative as well as floral characters. *A* and *B* have a dominant white flower colour (with a network of different strength), *L* and *M* are red-flowered. The *A* line is rather low and early, the other lines being more tall and late. The three independent lines, *D*, *G* and *I*, finally, are also rather dissimilar and do not show any particular resemblance to the other lines.

Consequently, as no connection can be traced between morphology and group delimitation, it remains to be seen whether the geographical origin is of importance. Four of the twelve lines, *viz*. *F*, *J*, *E* and *G*, were collected at the same locality at Andrarum, eastern Skåne. At this locality the *Galeopsis* population was markedly polymorphous, consisting not only of various *Tetrahit* types but also of different forms belonging to *G. bifida*, *speciosa* and *Ladanum*. It is interesting to note that three of the *Tetrahit* lines from Andrarum (*F*, *J* and *E*) were found to belong to the first sterility group, but, as reported above, the fourth line, *G*, is quite different with respect to the constitutional causes of sterility. In addition to *F*, *J* and *E*, the lines *X* and *C* belong to the same sterility group. Of these lines *X* was collected at Hörröd, a locality situated only a few miles from Andrarum. Consequently, the geographical origin of four of the five lines in the group is closely similar. The fifth line, *C*, on the other hand, was obtained from the Botanical Garden of Riga (Latvia), and is therefore in all probability of quite a different origin from the other lines in the same group.

The second group of lines, similar with regard to the causes of sterility, consists of *A*, *B*, *L* and *M*. Of these the line *A* was obtained from the Botanical Garden of Tabor (Czechoslovakia), *M* from the Botanical Garden of Eastborne (England). The remaining two lines were collected in eastern Skåne, *B* at Rörum, *L* at Vitaby. As regards the lines *D*, *G* and *I*, each representing a special sterility type, it has been mentioned above that *G* was obtained from Andrarum, eastern Skåne. The line *D* has a similar origin (Kivik, eastern Skåne), while the line *I* was collected at Gothenburg.

According to the data recorded above, it is evident that the geo-

graphical origin is of little or no importance as regards the sterility constitution. Lines from exactly the same locality, however, seem to show a tendency to be similar in constitution as was the case with three of the four lines from Andrarum. However, the fourth of these lines, *G*, being quite different, demonstrates that an identical origin is no guarantee of a similar constitution. On the other hand, lines of quite different geographical origin may evidently be fertile with each other and react in the same way with other lines.

D. CORRELATION BETWEEN REACTION RATIO AND POLLEN FERTILITY.

From the survey given in Table 3 (p. 125) it will be seen that the fact that two lines are fertile with each other is no guarantee whatever that they will react in the same way in crosses with other lines. Thus it often happens that the lines 1 and 2 as well as 1 and 3 are fertile with each other though 2 and 3 give sterile F_1 hybrids. Under such circumstances all attempts to divide the lines into intrafertile but intersterile groups are useless.

However, when, as in the present case, a material is available in which the lines have been crossed in all directions possible, the degree of similarity between two lines may easily be estimated by testing the extent to which the lines react differently or in the same way with other lines. Between each member of a line pair and the remaining ten lines 10 cross combinations are possible. If the two lines compared react in the same way with all the other ten lines, such a pair is characterized by the ratio 10 (alike) : 0 (differently). According to Table 3 and the previous discussion, only three of the twelve lines tested (*F*, *J* and *X*) behave in exactly the same way as regards their reactions with the other lines. Thus, the line pairs *F*—*J*, *F*—*X* and *J*—*X* are all characterized by the ratio 10 : 0. In other cases, in which the similarity between the lines compared is less complete, the ratio 10 : 0 is altered to 9 : 1, 8 : 2, 7 : 3 and so on. Concerning lines which are fertile with each other, the most extreme difference in the mode of reaction is represented by the lines *A* and *E*. These lines are apparently fertile with each other, it is true, but their reaction with other lines is characterized by the ratio 2 : 8, *i. e.* *A* and *E* behave in the same way only in two cases and react differently in 8 cases out of 10. — A still greater constitutional dissimilarity is found between *C* and *M*, which react similarly only in one case and differently in 9 cases. Moreover, these lines are sterile with each other. Below the numerical ratio, denoting

the mode of reaction of two lines in combination with the other lines, will be referred to as the *reaction ratio*. Theoretically, in the present material the reaction ratio may vary from 10 : 0 to 0 : 10, but the extremes actually found are 10 : 0 and 1 : 9.

The combinations in Table 3 have been divided into two categories, *viz.* lines which are fertile with each other and lines giving sterile F_1 generations. As is evident from the table the reaction ratios in the former category are usually higher than in the latter. The average proportion is in the first case 6,73 : 3,27 and as regards the sterile category 3,75 : 6,25. The difference between these ratios is significant as is immediately evident by a comparison between the series formed by the two categories. As may be easily controlled by means of the χ^2 method, the probability that the distributions in the two categories represent the same type is much less than 0,01. Thus, it may be concluded that if two lines are fertile with each other, it is really possible to predict something about their mode of reaction with other lines. However, according to the proportion 6,73 : 3,27 in the present material, the odds are only about 2 : 1 that the lines will react in the same way when crossed to a third line. If, on the contrary, two lines are sterile with each other it is rather probable that they will react differently in crosses with a third line. According to the ratio 3,75 : 6,25 the probability of a different reaction is almost twice as great as that of a similar reaction.

Judging from the fertility or sterility of the F_1 hybrids, it is therefore possible to draw conclusions as to the probable mode of reaction of the parent lines in crosses with other lines. On the other hand, if it is known how two lines react with other lines, it is evidently possible, to a certain extent, to judge whether these two lines will give sterile or fertile F_1 hybrids with each other. An interesting point is that this correlation was found to be *gradual, i. e. there is a clear positive correlation between the degree of fertility of the F_1 hybrids and the degree of similarity with which the parent lines react with other lines.* This is evident from Table 4, showing the correlation between the reaction ratios and the pollen fertility of the F_1 generations. This table represents a combination of the percentage values in Diagram 1 and the reaction ratios in Table 3. On account of the limited number of variates the material in Table 4 has been divided in five double classes. Thus, the class 10—0 and 9—1 comprises such pairs of lines which either react identically in all crosses with the other lines or equally in 9 cases of 10. In Table 3 six pairs of this kind are represented, *viz.* *A—M*, *B—M*, *F—J*, *F—X*, *J—X* and *L—M*. The corresponding F_1

generations, *i. e.* $A \times M$, $B \times M$, $F \times J$ etc., had all between 95 and 100 per cent good pollen, the total average being 97,5. In the next class (8—2 and 7—3) the average pollen fertility was found to be somewhat lower, the value being 92,5 per cent. In the other classes there is a continuous decrease down to 65,8, which value is found in the class 2—8 and 1—9. This very marked correlation strikingly demonstrates that *in respect to the causes of sterility the degree of pollen fertility in a certain F_1 combination is a good expression of the degree of constitutional similarity between the parents.* Thus, if a certain F_1 generation is found to have a very high degree of pollen fertility, it is highly probable that the parent lines have such a similar constitution that in crosses with other lines they will react completely or pre-

TABLE 4. *Correlation between reaction ratio and pollen fertility of the F_1 generations.*

Reaction ratio	Percentage of good pollen:											n	M
	50	55	60	65	70	75	80	85	90	95	100		
10—0 and 9—1											6	6	97,5
8—2 » 7—3							1	—	1	7	4	13	92,5
6—4 » 5—5	1	1	—	3	—	—	—	3	4	3		15	82,5
4—6 » 3—7	1	1	2	1	4	6	—	—	4	1		20	76,3
2—8 » 1—9	2	3	2	2	1	—	1	—	—	1		12	65,8

dominantly in the same way. If the F_1 generation is slightly sterile this is due to one or more minor differences between the parents, which also cause them to react somewhat differently with other lines. If, finally, the F_1 hybrids are markedly sterile (*i. e.* to about 50 per cent) this is due to rather profound differences between the parent lines, which are also responsible for an essentially different mode of reaction with other lines.

III. A CASE OF INTRASPECIFIC STERILITY IN GALEOPSIS SPECIOSA.

The investigations of intraspecific sterility in *Galeopsis* have hitherto been confined to *G. Tetrahit*. The following case of intraspecific sterility, clearly due to genotypical causes, was met with in *G. speciosa*. In 1924 seeds were collected of a *G. speciosa* type from Kivik, eastern Skåne. Under natural conditions this type was evidently a cross fertilizer, and during the first years of culture the seed production on isolation was

often poor, and in some years it was necessary to breed the new generation from seeds after open pollination. In 1931 pollen fertility was studied in a progeny of an open pollinated mother plant. To my surprise the 29 plants examined fell into two distinct categories, *viz.* 13 plants with 85—100 per cent good pollen and 16 plants with a percentage varying between 30 and 70. (The variation in this case is represented in Table 5, progeny No. 15). In order to study this case more closely four progenies were raised in the following year, one from a fertile and three from partially sterile mother plants. The first-mentioned progeny (No. 1) consisted of 16 plants, 14 of which had 95—100 per cent, the remaining two plants having 90—95 and 85—90 per cent good pollen respectively. The other three progenies (Nos. 16, 17 and 18), on the contrary, showed a marked variation and a bimodal segregation into fertile and partially sterile individuals.

Already from this result it was rather clear that the sterility in this case was genotypically controlled. In order to obtain more reliable values the fertility variation in progenies (after isolation) from fertile and sterile mother plants was further studied in the following five years. During the progress of this work it has become evident that this *speciosa* sterility is indeed genotypically caused, but it is also sometimes strongly influenced by environmental conditions. This is in part reflected by the fact that the limit between sterile and fertile combinations is sometimes continuous. Further, it occasionally happens that repeated determinations of the pollen percentage in a certain plant give rather variable results. Thus, for instance, the mother plant of progeny 24 (Table 5) was examined four times, the percentage values 98, 65, 63 and 47 being obtained, and a similar variation has been observed in several other cases. In spite of these exceptions it can be said that, as a rule, repeated counts from the same individual give similar results.

It should not be necessary to give a detailed account of the relationship between the progenies represented in Table 5. Each year, however, progenies were raised from fertile as well as partially sterile mother plants. The progenies of the former mainly consisted of fertile individuals, the partially sterile mother plants, on the contrary, were found to segregate in fertile and partially sterile daughter plants. In a few cases the pollen percentage of the mother plant has not been determined, but in such cases the fertility variation in the progeny clearly indicates the category to which it is to be referred. Table 5 gives not only the pollen percentage of the mother plant but also that of the grandmother plant. The latter value is of interest because in the

TABLE 5. *Galeopsis speciosa. Pollen fertility in progenies of fertile and partially sterile mother plants.*

Progeny No.	Year	Field number	Pollen percentage of the mother plant	Pollen percentage of the grand mother plant	Percentage of good pollen: 10	20	30	40	50	60	70	80	90	100	n
1	1932	204	?	?									1	15	16
2	1933	98	94	?										8	8
3	»	99	95—100	?										10	10
4	1934	189	95—100	94					1	—	1	1	1	9	13
5	1935	136	98	52						1	1	—	—	27	29
6	»	139	84	95—100							1	—	1	30	32
7	»	140	86	?					1	—	—	—	2	16	19
8	1936	110	95—100	68					1	1	—	1	2	14	19
9	1937	135	56	95—100						1	1	—	—	18	20
10	»	136	82	»										16	16
11	»	137	95—100	»										16	16
12	»	138	?	»							1	—	—	9	10
13	»	139	?	»							1	—	1	8	10
14	»	140	?	82										10	10
1—14, total, absolute values									3	3	6	2	8	206	228
1—14, » , per cent									1,3	1,3	2,6	0,9	3,5	90,4	100
15	1931	151	?	?				1	5	8	2	—	1	12	29
16	1932	202	?	?					1	4	3	—	3	2	13
17	»	203	?	?						7	1	—	—	4	12
18	»	205	?	?					1	8	1	—	1	5	16
19	1933	96	55	?					1	2	—	—	—	6	9
20	»	97	55	?					2	2	—	—	—	2	6
21	1934	186	43	55	2	—	1	2	13	10	4	4	13		49
22	»	187	52	»			1	5	8	10	8	3	15		50
23	»	188	51	»			1	2	8	8	7	3	20		49
24	1935	133	68	43				2	8	6	2	—	17		35
25	»	134	60	»				4	10	12	1	1	18		46
26	»	135	57	»				2	5	1	—	—	2		10
27	»	137	58	51				2	7	2	—	2	9		22
28	»	138	74	»				1	2	—	—	4	8		15
29	1936	109	53	68			1	4	2	4	1	—	10		22
30	1937	132	56	53				1	4	4	2	—	9		20
31	»	133	48	»				1	6	—	—	—	12		19
32	»	134	79	»					2	1	—	—	17		20
15—32, total, absolute values					2	—	5	36	106	65	25	22	181		442
15—32, » , per cent					0,5	—	1,1	8,1	24,0	14,7	5,7	5,0	40,9		100

case of progenies, segregating in fertile : semi-sterile, not only the mother but also the grandmother should be partially sterile. This was found to be true of all the 12 progenies in which both these values are known. — On the other hand, fertile, non-segregating progenies must have fertile mother plants but may have fertile or partially sterile grand-

mothers. In the main this is true of the material represented in the first part of Table 5.

There is one obvious exception, however. The mother plant of progeny 9 had an average of only 56 per cent good pollen, though 18 of the 20 daughter plants were clearly fertile. That indicates that in this case the reduced pollen fertility of the mother plant was caused exclusively by unfavourable environmental conditions and not, as in the other cases, by heterozygosity for sterility factors. This assumption is supported very strongly by the fact that the grandmother plant had been found to be perfectly fertile. Also a few of the other individuals giving fertile progenies had a somewhat reduced fertility, the pollen percentage, however, was in no case lower than 82. This evidence of a reduced fertility due to environmental influences is in keeping with the fact that about 10 per cent of the daughter plants of fertile mother individuals were found to have less than 90 per cent good pollen. Most probably the amount of poor pollen in these plants is exclusively due to disturbing external influences. However, the important feature of these progenies (Nos. 1—14) is the fact that not less than 90,4 per cent of the daughter plants had quite good fertility, the percentage of good pollen ranging from 90 to 100.

The progenies of partially sterile mother plants (Table 5, Nos. 15—32) vary in quite a different way, showing a clearly bimodal distribution with one maximum at 90—100 and the other at 50—60. The limit between these modes is not sharply defined, but a comparison with the progenies of fertile mother plants facilitates an estimation of the relative frequency of genotypically sterile and fertile plants. Since about 10 per cent of the descendants of fertile mother plants were found to be more or less sterile, due to environmental influences, it is probable that the same influences act on the progenies of partially sterile mother plants. According to Table 5, 59,1 per cent of the plants in these progenies have less than 90 per cent good pollen, but according to the previous argument about 10 per cent of these plants are sterile simply on account of environmental influences. This being the case, the ratio of genotypically fertile and sterile individuals would be approximately 47 : 53. These percentage values correspond very closely to the ratio 1 : 1. Under such circumstances it is very probable that, in the main, this sterility is inherited in the same way as the classical cases of semi-sterility. In such cases, which have also been observed in *G. Tetrahit* (MÜNTZING, 1929, 1930 a, 1932 a), sterility is due to a bifactorial (or bistructural) difference, causing two of the four types of gametes to be lethal and to appear as

empty pollen grains and aborted embryo sacs. At any rate, judging from the material represented in Table 5, it can scarcely be doubted that *the intraspecific sterility in G. speciosa is mainly due to causes of the same kind as those responsible for the corresponding sterility phenomena in G. Tetrahit.*

IV. CYTOLOGICAL INVESTIGATIONS IN GALEOPSIS TETRAHIT.

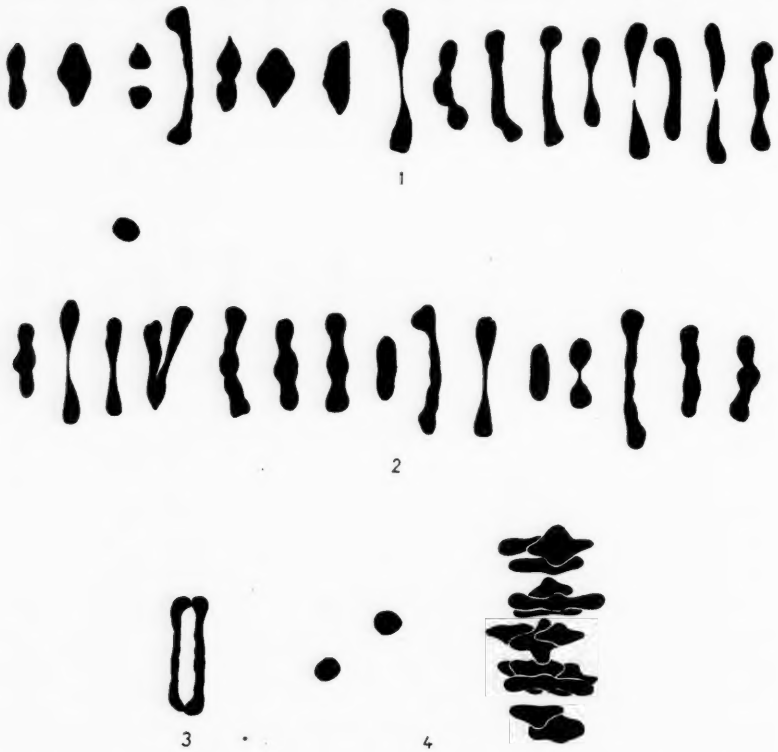
1. CHROMOSOME PAIRING IN PURE LINES.

Hitherto only a few cytological observations have been made concerning the mode of meiosis in pure lines of *G. Tetrahit*. In a previous paper (MÜNTZING, 1930 a, pp. 233—234) these observations are chiefly confined to the statement that 32 is the definite or probable chromosome number (2n) of all the lines tested, *viz. A, B, C, D* and *X*. For comparison with the mode of meiosis in the intraspecific hybrids these observations have now been extended, the following results having been obtained.

By means of direct counts it has been verified that 32 is the somatic number in the lines *B, C* and *D*. Moreover, the same number has now been found in the lines *E, F, L* and *G*. Additional, though indirect, evidence that $2n = 32$ is the typical number of all the *Tetrahit* lines was acquired during the cytological studies of several F_1 generations. In all cases in which it was possible to count the chromosomes, the number was found to be 32. These studies alone furnish strong evidence that the lines *B, C, D, F, G, I* and *M* have $2n = 32$. As just mentioned, most of these lines were studied directly, but the F_1 counts demonstrate that also *I* and *M* behave like the other *Tetrahit* lines. The only one of the 12 lines used for the crosses which has not yet been studied cytologically, directly or indirectly, is the line *J*. There is no reason to believe, however, that this line should have a deviating chromosome number, especially since *J* was found to be identical with *F* and *X* with respect to the sterility reactions.

At first metaphase the 32 chromosomes typical of the *Tetrahit* lines generally occur in the shape of 16 bivalents (Fig. 1). In the majority of these bivalents the chromosomes are united by a terminal chiasma. In less frequent cases the bivalents are ring-shaped with two chiasmata. In a few cases four of the chromosomes were observed to form a trivalent + a univalent instead of two bivalents. Consequently, the total configuration formed in such a case consists of $1_{III} + 14_{II} + 1_{I}$.

Such an exceptional metaphase group from the line *E* is represented in Fig. 2. In the same line, among hundreds of groups with exclusively bivalents, a single true quadrivalent was observed (Fig. 3). Judging from all the observations in the pure lines, such tri- and quadrivalents



Figs. 1—4. I—M configurations in pure lines of *Galeopsis Tetrahit* (Figs. 1—3 from *T—E*, Fig. 4 from *T—L*). — Fig. 1, the typical chromosome complement, consisting of 16 bivalents; Fig. 2, an exceptional group with $1_{III} + 14_{II} + 1_{I}$; Fig. 3, a quadrivalent; Fig. 4, $15_{II} + 2_{I}$ (non-conjunction in one chromosome pair, univalents of equal size). — × 4500 (as in all the following figures).

are quite rare, and they certainly occur in less than one per cent of the metaphase groups.

The occurrence of univalents, however, is much more frequent, and especially the simultaneous presence of two unpaired chromosomes. Such univalents were always observed to be about equal in size and

evidently result from non-conjunction in one of the chromosome pairs, the other chromosomes, in all cases controlled, forming 15 bivalents. Thus, the total configuration will be $15_{II} + 2_{I}$ as in Fig. 4, representing a metaphase group from the line *L*.

The frequency of univalents was determined in 7 different pure lines, *viz. B*, *C*, *D*, *E*, *F*, *G* and *L*. The results of these countings are summarized in Table 6. As shown in the table, altogether 814 I—M groups were observed, and of these 92,38 per cent had no visible univalents, the remaining 7,62 per cent containing 1—4 univalents. In the

TABLE 6. *Frequency of univalents in pure lines of G. Tetrahit.*

Line	Fix.-No.	Prep.-No.	Number of univalents outside the I—M groups: 0	1	2	3	4	Number of I—M groups observed	Percentage of I—M groups with 1 or more univalents
B	389	1	20					20	0
C	375	1	110	1	4			115	4
D	388	1	30	—	3			33	9
D	»	2	46	—	3			49	6
D, total ...	»	1+2	76	—	6			82	7
E	379	1	90	3	7			100	10
E	»	2	87	3	5			95	8
E, total ...	»	1+2	177	6	12			195	9
F	440	1	110	1	1			112	2
G	441	1	47	1	1			49	4
L	400	1	100	—	14	—	1	115	13
L	»	2	44	—	8	—	3	55	20
L	460	1	68	—	3			71	4
L, total ...	400+460	1+2+1	212	—	25	—	4	241	12
All the lines:			752	9	49	—	4	814	7,62

latter category the most frequent class is represented by cells with 2 univalents. In a few cases 4 univalents were observed in the same cell, these evidently being the result of non-conjunction in two chromosome pairs. In 9 cells only one univalent could be distinguished. It is possible that the configuration in these cells is $1_{III} + 14_{II} + 1_{I}$, as shown in Fig. 2. It is also possible, however, that some of these cells really contain two univalents, though only one of them was detected, the other being hidden among the bivalents.

Though, according to Table 6, the average percentage of metaphase groups with univalents is 7,62, there is a rather marked variation in different lines and different preparations, the percentage values ranging from 0 to 20. There are no significant line differences, however, and

the variation is evidently partly due to the limited number of metaphase groups observed, partly to disturbing environmental influences. The latter circumstance is especially evident in the case of line *L*, in which fixation No. 400, prep. 2 gave the value 20 per cent, whereas fixation No. 460 gave an average of 4 per cent. The standard errors of these percentage values (calculated on the basis of the average percentage, 11) are 4,47 and 3,93 respectively. The exact difference is $15{,}77 \pm 5{,}95$ and D/m = 2,65. As this D/m value is rather high, it is very probable that the difference in this case is due to some special external influence.

2. CHROMOSOME PAIRING IN THE F_1 COMBINATIONS.

A. FREQUENCY OF UNIVALENTS.

Hitherto nine different F_1 generations, chosen at random, have been cytologically examined. In the first place the frequency of univalents was determined in the same way as in the pure lines. As is evident from the data summarized in Table 7, *the percentage of metaphase groups with univalents is in all the F_1 combinations higher than in any of the pure lines.* Thus it is quite evident that the occurrence of a variable number of univalents is quite a typical feature of the F_1 hybrids. However, the percentage values fall within rather wide limits, and in the present material there is a variation from 18 to 93 per cent. In the pure lines the average values ranged from 0 to 13. Thus, between the lines and F_1 combinations the difference in univalent frequency is fully significant.

It is equally certain, however, that *different F_1 generations are characterized by different degrees of univalent frequency.* This frequency, for instance, was found to be much lower in the $B \times C$ hybrids than in $D \times I$. In the former hybrids only 18 per cent of the metaphase groups was found to contain one or usually two univalents. This average value is based on four different slides from both the reciprocal combinations (cf. Table 7). Considering the relatively low number of variates, these slides gave rather similar values, *viz.* 21, 24, 18 and 13 per cent. — In the $D \times I$ hybrids, on the other hand, all values obtained were essentially higher. Three slides of fixation No. 201 gave the figures 91, 93 and 92 per cent of metaphase groups with one or several univalents. However, another fixation (No. 203) of the same hybrid gave an essentially lower average number, *viz.* 46 per cent. In spite of the poor agreement between the latter two fixations it is highly probable

that the $B \times C$ hybrids have a significantly lower frequency of univalents than the F_1 plants of the cross $D \times I$.

Also in another case, the cross $B \times G$ and reciprocally, two different fixations gave rather different percentage values. In fixation No. 387

TABLE 7. *Frequency of univalents in intraspecific hybrids of G. Tetrahit.*

Cross combination	Fix.-No.	Prep.-No.	Number of univalents outside the I—M groups: 0	1	2	3	4	5	6	7	Number of I—M groups observed	Percentage of I—M groups with 1 or more univalents	Percentage of good pollen
A × I.....	207	1	40	6	4						50	20	69
»	»	2	75	18	9	1	2				105	29	»
» , total	»	1 + 2	115	24	13	1	2				155	26	69
B × C	376	1	79	7	14						100	21	56
»	»	2	19	2	4						25	24	»
C × B	380	1	41	2	7						50	18	77
»	»	2	60	6	3						69	13	»
B × C ..... and	376 +												
C × B, total	380		199	17	28						244	18	67
B × G	387	1	10	20	78	30	5	2	1		146	93	75
G × B	209	1	91	36	25	2	3				157	42	»
D × I.....	201	1	10	77	20	4	1	1			113	91	64
»	»	2	8	79	24	4					115	93	»
»	»	3	8	62	29	4					103	92	»
»	»	1 + 2 + 3	26	218	73	12	1	1			331	92	»
»	203	1	46	30	5	1	1				83	44	77
G × E	370	1	81	35	11	3	1				131	38	87
»	»	2	82	36	15	1	—	—	—	1	135	39	»
» , total	»	1 + 2	163	71	26	4	1	—	—	1	266	39	87
G × F	464	1	37	33	6	3	1				80	54	98
G × J	211	1	80	13	11	1	1				106	25	92
»	»	2	83	17	10	2					112	26	92
» , total	»	1 + 2	163	30	21	3	1				218	25	92
L × G	212	1	16	6							22	27	87
»	»	2	55	18	3	1					77	29	»
» , total	»	1 + 2	71	24	3	1					99	28	87
I × M.....	374	1	24	27	9						60	60	55
Total of all F_1 generations:			945	530	287	57	15	3	1	1	1839	48,61	—

as much as 93 per cent of the metaphase groups contained univalents, the corresponding value of fixation No. 209 being only 42 per cent. It should be observed, however, that in this case the fixations were from different years, and, further, one of them was made from a $B \times G$ plant, the other from the reciprocal combination, $G \times B$. Thus, different fixations *may* give rather deviating values, while different slides

from the same fixation generally present a very similar frequency of univalents (cf. Table 7). In spite of the variation between different fixations, however, it is quite evident that different F_1 combinations differ in regard to the univalent frequency. The cross $B \times C$ has already been mentioned as an example of a low frequency, the frequency in the crosses $D \times I$ and $B \times G$, on the contrary, being very high. More intermediate numbers are evidently represented by the combinations $G \times E$, $G \times J$ and others.

Adding all the values from the nine F_1 combinations it is found that the average frequency of metaphase groups with univalents is 48,61 per cent whereas the corresponding value of the pure lines is not higher than 7,62 per cent. The distribution in the two series (Tables 6—7, at the bottom) is so different that the significance of this difference is at once obvious without any special statistical treatment. Further, it is noteworthy that *one* is the most frequent number of univalents in the F_1 hybrids, while in the pure lines the univalents generally occur in *pairs*. However, in the hybrids, too, there are often two univalents in the same cell, less frequently three or four. A higher number than four was observed in only 5 cases out of 1839.

The F_1 generations evidently differ also with regard to the average number of univalents per cell. The $B \times C$ plants behave almost like a pure line, the univalents generally appearing in pairs. In the $D \times J$ hybrids, on the other hand, about $^2/_3$ of the metaphase groups contain *one* univalent.

B. CONFIGURATIONS IN DIFFERENT F_1 HYBRIDS.

On account of the frequent occurrence of univalents in the F_1 hybrids it seemed desirable to analyse, as far as possible, the total chromosome configurations, especially in metaphase groups with univalents. In some good fixations this was possible to a certain extent, the following results being obtained.

In the hybrids $A \times I$, $G \times E$ and $G \times J$ no metaphase groups have been completely analysed, but in all these combinations several cases of the simultaneous occurrence of one univalent and one trivalent were observed. Thus the configurations in these hybrids were probably $1_{III} + 14_{II} + 1_I$. In the following cases more definite information could be acquired:

a) $G \times B$. — Also in this hybrid the simultaneous occurrence of uni- and trivalents was observed. Two complete metaphase groups

contained $1_{III} + 14_{II} + 1_{I}$, a third group had $1_{III} + 13_{II} + 3_{I}$ (Fig. 13) and a fourth probably $15_{II} + 2_{I}$.

b) $G \times F$. — In this hybrid combination five groups could be analysed, two of which had 16_{II}, two probably $1_{III} + 14_{II} + 1_{I}$ and the fifth group $1_{IV} + 14_{II}$.

c) $I \times M$. — Three metaphase groups contained 16_{II}, $15_{II} + 2_{I}$ and $1_{III} + 14_{II} + 1_{I}$ respectively.

d) $B \times C$. — This F_1 combination is especially interesting, partly because it is markedly sterile (M = 56 per cent), partly because the inheritance of sterility in this cross and its connection with disturbed segregation ratios has been subjected to special studies (MÜNTZING, 1930 a, 1932 a). In the paper of 1932, two metaphase groups are reproduced, both containing 16 bivalents. One of these groups was from a fertile, the other from a sterile F_3 plant. On account of these and other similar observations the conclusion was drawn that there are no cytological complications in this cross and probably not in other hybrids within the species either. The present investigation, however, shows that the latter conclusion at least is wrong, and as to the $B \times C$ hybrids the frequency of univalents was found to be somewhat higher than in the pure lines. The difference, however, is very slight (cf. Table 7), and meiosis in this hybrid combination is in fact strikingly regular.

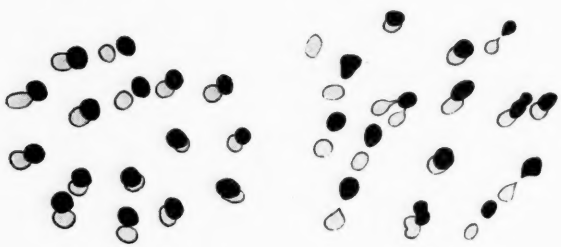
A study of some good slides of this F_1 hybrid demonstrated, indeed, that the great majority of the metaphase groups consist exclusively of bivalents. Not a single quadrivalent could be detected, and if such associations really occur, the frequency must be very low. Judging from all the observations, only bivalents and a low frequency of univalents occur. In a few cases complete groups were analysed and found to consist either of 16_{II} or $15_{II} + 2_{I}$, a group of the latter kind being represented in Fig. 19. — Thus, the conclusion previously drawn (MÜNTZING, 1932 a) that meiosis in this hybrid is regular, is in the main verified by the present observations.

e) $D \times I$. — The hybrids between D and I represent the F_1 combination hitherto most thoroughly investigated. From the fixations 201 and 203 (cf. Table 7) some good slides were obtained, rendering an analysis of a relatively large number of metaphase groups possible. As the fixations mentioned represented rather different frequencies of univalents, it is necessary to consider each of them separately. In one slide of fixation No. 201, in which the percentage of I—M groups with univalents was as high as 91, 19 metaphases could be analysed. These

5

6

7



8 9

10a 10b

11 12

metaphases represented six different configurations, occurring in the following frequency:

16_{II} : 1 cell; $1_{III} + 12_{II} + 5_{I}$: 1 cell;
$1_{III} + 14_{II} + 1_{I}$: 13 cells; $2_{III} + 12_{II} + 2_{I}$: 2 cells;
$1_{III} + 13_{II} + 3_{I}$: 1 cell; $2_{III} + 11_{II} + 4_{I}$: 1 cell.

The normal configuration of the pure lines, 16_{II}, only occurred in one single cell. The other configurations are characterized by the simultaneous occurrence of univalents and trivalents, the number of trivalents being 1 or 2, the number of univalents ranging from 1 to 5. According to Table 7, however, there is generally only *one* univalent in the I--M groups of this fixation, this being the case in 66 per cent of the cells. This is in excellent agreement with the 19 configurations observed, 13 of which, *i. e.* 67 per cent, were found to contain one univalent. The most important fact, however, is that in all these cells there is quite a definite configuration, *viz.* $1_{III} + 14_{II} + 1_{I}$. This fact makes it highly probable that in this configuration *the trivalents and univalents are always represented by the same chromosomes.*

Further information as to the cytology of this hybrid combination was obtained from fixation No. 203, in which the frequency of univalents (46 per cent) was lower than in the previous fixation. In one slide of fixation 203 twenty-five metaphase groups could be analysed, which were found to represent the following configurations:

16_{II} : 8 cells; $1_{IV} + 1_{III} + 12_{II} + 1_{I}$: 1 cell;
$1_{III} + 14_{II} + 1_{I}$: 12 » ; $15_{II} + 2_{I}$: 1 » ;
$1_{IV} + 14_{II}$: 3 » .

As in the previous fixation, $1_{III} + 14_{II} + 1_{I}$ is evidently the most frequent configuration. Two other configurations also contained univalents, but on an average cells without univalents were about equally numerous. This is an accordance with the relatively low frequency of univalents in this fixation (46 per cent).

Upon closer examination most of the groups without univalents were found to consist of 16 bivalents, but in a few cases there occurred well-defined quadrivalents. Of 21 cells without univalents 9 certainly

Figs. 5—12. I—M configurations in hybrids between the *D* and *I* lines. — Fig. 5, the most frequent configuration, $1_{III} + 14_{II} + 1_{I}$; Fig. 6, $1_{IV} + 1_{III} + 12_{II} + 1_{I}$; Fig. 7, $2_{III} + 12_{II} + 2_{I}$; Fig. 8, 16_{II} in polar view; Fig. 9, polar view with $1_{III} + 14_{II} + 1_{I}$; Fig. 10, 6 trivalents and corresponding univalents from different metaphase groups; Fig. 11, 1 trivalent and 5 univalents from the same cell, the univalents representing different sizes; Fig. 12, 3 quadrivalents from different cells.

contained bivalents exclusively. In three cells there was a sure quadrivalent and in the remaining 9 cells associations were observed which were possibly quadrivalents, but which may also have been made up of two bivalents. Thus, cells with 16_{II} are probably more common than those with $1_{IV} + 14_{II}$. Most frequent, however, is the configuration $1_{III} + 14_{II} + 1_{I}$, which is quite typical of this F_1 combination.

Judging from the configurations, the difference between the fixations consists in a somewhat higher chiasma frequency in No. 203 than in No. 201. In No. 203 four of the chromosomes may relatively often form a continuous association, the corresponding chromosomes in No. 201, as a rule, only being able to form a trivalent + a univalent.

Some typical pictures showing the chromosome pairing in this F_1 combination are reproduced in Figs. 5—12. Fig. 5 shows the most frequent configuration, $1_{III} + 14_{II} + 1_{I}$. In Fig. 6 the chromosome complement consists of $1_{IV} + 1_{III} + 12_{II} + 1_{I}$, and in Fig. 7 there are $2_{III} + + 12_{II} + 2_{I}$. Figs. 8 and 9 represent two metaphase groups in »polar view», Fig. 8 showing the relatively rare chromosome complement of 16_{II}, Fig. 9 containing the typical configuration $1_{III} + 14_{II} + 1_{I}$. In Fig. 10 there are 6 different trivalents and the corresponding univalents from groups with $1_{III} + 14_{II} + 1_{I}$. The first four trivalents (with univalents) from the left are from fixation No. 203, the two groups to the right from the other fixation (No. 201). Within each fixation the univalents give the impression of being of the same size. As emphasized above, the univalent in these cases certainly represents a particular chromosome, which seems to be rather small. — Fig. 11 shows some of the chromosomes from an exceptional metaphase group containing 5 univalents and one trivalent in addition to the other chromosomes. From the figure it is quite evident that the univalents in this case represent different sizes. Fig. 12, finally, shows three quadrivalents of different types from three different metaphase groups.

C. THE RELATIVE SIZE OF THE UNIVALENTS IN THE HYBRIDS BETWEEN THE *B* AND *G* LINES.

In the course of the cytological work it was observed that in those hybrids and in those cells in which there are more than one univalent in the metaphase groups, these univalents often differ markedly in size. On the other hand, in the pure lines two univalents occasionally occurring in the same cell were always found to be of about the same dimensions. Further, if a certain F_1 combination is characterized by

the occurrence of *one* univalent in most of the cells, this univalent, judging from its size, always seems to represent the same chromosome. As mentioned above, this is probably the case, for instance, in the $D \times I$ hybrids.

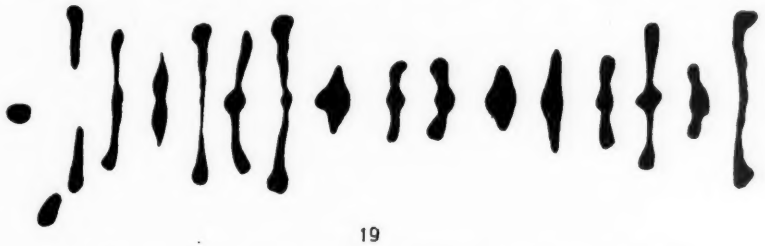
In order to get an exact verification of these observations some measurements were performed. These measurements were facilitated by the fact that in *Galeopsis* the univalents at the I—M stage are either quite spherical or slightly elongated. The measurements were carried out, first, by making camera lucida drawings at the highest possible magnification ($\times 6750$) and then by measuring the drawings with a ruler graduated in $^1/_2$ millimetres. The values to be discussed in the following represent the average between the longest and shortest diameter.

The most distinct differences in univalent size were observed in the hybrids between the lines *B* and *G*. In this F_1 combination the frequency of univalents is also high, as previously mentioned, reaching the value of 93 per cent in one fixation and 42 per cent in another (cf. Table 7). The number of univalents per metaphase group varied between 0 and 6. In fixation No. 387 most of the cells contained *two* univalents. The next category in frequency, the rate of frequency being less than half that of the first category, however, consisted of cells with *three* univalents. In both these categories the univalents were found to be strikingly different in size. Some typical groups with two univalents are represented in Figs. 14—15 and in these, as in all other cells containing two univalents, there is no hesitation as to which of the chromosomes is the largest one. In the cells with three univalents these almost always represent three different sizes, as is the case in Figs. 13 and 16. The former group could be completely analysed and was found to consist of $1_{III} + 13_{II} + 3_I$. — Some other configurations from the same F_1 have already been mentioned above (p. 141). — Fig. 17 represents a group with as many as 5 univalents, partly differing in size. In Fig. 18, finally, there are 6 multivalents (all of them probably trivalents) and the corresponding univalents from the same cells. In the cases with 3 univalents these evidently represent different size-groups.

The results of the univalent measurements have been summarized in Tables 8 and 9, these tables containing the values obtained from the $B \times G$ hybrid and the results of quite comparable measurements from four pure lines. The units in the tables are millimetres. The absolute size of the univalents may be obtained by division with the degree of magnification, 6750.

13
14
15
16
17
18

The values of the pure lines are exclusively based on cells, exceptionally containing two univalents. In all, 46 such pairs of univalents from the lines *C*, *D*, *E* and *L* were observed and measured.



19

Fig. 19. I—M group from a $B \times C$ hybrid, showing $15_{II} + 2_{I}$.

The different lines (and fixations) gave rather similar values. Apart from the limited number of variates the differences present are probably caused by a slightly different treatment in fixation and staining.

TABLE 8. *Size of univalents in pure lines and in the F_1 hybrid $B \times G$.*

Line or F_1 generation	Average diameter of the univalents: 3,5	4,0	4,5	5,0	5,5	6,0	6,5	7,0	7,5	8,0	n	M ± m
C			1	3	4						8	5,19
D			1	3	4	1	2	1			12	5,63
E			1	1	7	9	7	1			26	5,94
L			4	10	24	8					46	5,39
Total			7	17	39	18	9	2			92	5,56 ± 0,06
B × G, F_1, small univ.	1	2	14	32	11	3					63	4,97 ± 0,06
» » large »			1	1	6	10	28	15	1	1	63	6,43 ± 0,07
Total	1	2	15	33	17	13	28	15	1	1	126	5,70 ± 0,08

It may also be possible that certain chromosome pairs have a greater tendency to non-conjunction than others, this being combined with size differences between the lines. It seems more probable, however, that non-conjunction may occur in any chromosome pair and in about the

Figs. 13—18. I—M configurations in hybrids between the *B* and *G* lines. — Fig. 13, complete group with $1_{III} + 13_{II} + 3_{I}$, the univalents of different size; Figs. 14—15, I—M groups with two univalents, differing in size; Fig. 16, group with three univalents of different size (as in Fig. 13); Fig. 17, group with five univalents, partly differing in size; Fig. 18, six different multivalents (all or most of them = trivalents) and the corresponding univalents from the same cell.

same frequency. In such a case the different lines should give about the same average values as regards the size of the univalents.

According to Table 8 the average size of the univalents is $5{,}56 \pm 0{,}06$. About the same average size, or $5{,}70 \pm 0{,}08$ is characteristic of the univalents in the $B \times G$ hybrid. — This mean value, however, only refers to cells containing two univalents. — As just pointed out, these univalents in the $B \times G$ hybrids are of clearly different sizes and therefore it is possible to classify them as small and large ones. According to Table 8, the average value of the series formed by the small univalents is $4{,}97 \pm 0{,}06$, the corresponding value of the large univalents being $6{,}43 \pm 0{,}07$. It is possible that, in a few cases, the members of the two series have been confused, especially in cells in which the difference

TABLE 9. *The size differences of the univalent pairs in some pure lines and in the F_1 hybrid $B \times G$.*

Line or F_1 generation	0,0	0,5	1,0	1,5	2,0	2,5	3,0	n	Average difference	Average size	Difference in per cent of the average size
C	1	3						4	0,37	5,19	7,13
D	2	3	1					6	0,42	5,63	7,46
E	6	7						13	0,27	5,94	4,55
L	8	14	1					23	0,35	5,39	6,49
Total	17	27	2					46	$0{,}34 \pm 0{,}04$	$5{,}56 \pm 0{,}06$	$6{,}12 \pm 0{,}75$
B × G (R. 387)	1	6	12	27	11	5	1	63	$1{,}48 \pm 0{,}07$	$5{,}70 \pm 0{,}08$	$25{,}96 \pm 1{,}28$

measured was found to be slight. Such occasional mistakes would slightly exaggerate the average difference between the small and large univalents. In the present case, however, it is perfectly certain that the two univalents represent different size categories. This is especially evident from the distinctly bimodal distribution, representing the size of all univalents measured in cells of the $B \times G$ hybrid, containing exactly 2 univalents. According to Table 8, the number of variates in the different classes are the following: 1, 2, 15, 33, 17, 13, 28, 15, 1, 1. As is evident from the table, this series is also much more variable than the series formed by the total values of the pure lines.

With regard to univalent size the difference between the pure lines and the $B \times G$ hybrid is still more clear from the data presented in Table 9. In this table the size differences between the members of the univalent pairs are given. Thus, in the line *C* four cells were observed, containing two univalents. In three of these cells the difference was

0,5 units, in one cell 0,0, the average difference in this line thus being 0,37. The other values in the same table were obtained in the same way. Of all the 46 univalent pairs in the four pure lines 17 pairs consisted of univalents of exactly the same size, in 27 pairs the difference was 0,5 and only in 2 pairs as large as 1,0. The average difference in the pure lines is $0{,}34 \pm 0{,}04$, the corresponding figure of the $B \times G$ hybrid $1{,}48 \pm 0{,}07$, being more than four times as high.

Though the average size of the univalents in the pure lines and the $B \times G$ hybrid was about the same ($5{,}56 \pm 0{,}06$ and $5{,}70 \pm 0{,}08$ respectively) it is better to express the absolute differences in percentage of the average size than to compare these differences directly. In this way the value $6{,}12 \pm 0{,}75$ was obtained for the pure lines and $25{,}96 \pm 1{,}25$ for the $B \times G$ hybrid. Thus, *in the pure lines the difference in univalent size only amounts to approximately 6 per cent of the average size, the corresponding figure in $B \times G$ being more than four times as great.* The difference in between the two values is evidently quite significant [1].

In the $B \times G$ hybrid, using the same slides as before, measurements were also performed in 30 cells containing *three* univalents. In 24 of these cells all three univalents were of different sizes, in 5 cells the two smallest univalents were found to be equal and in 1 cell the two largest univalents were of the same size. As in most of the cells the univalents represent three sizes, it is evident that there are really three different size categories, even if the limits between these categories are not always quite clear-cut. Adding all the values of small, medium and large univalents the following three series were obtained:

	Average diameter of the univalents											
	3,5	4,0	4,5	5,0	5,5	6,0	6,5	7,0	7,5	8,0	n	M
Small univalents	1	5	15	9							30	4,53
Medium »			2	10	15	3					»	5,32
Large »					1	6	9	10	3	1	»	6,68

In view of the risk of erroneous classification, the differences between the average values are probably somewhat exaggerated. Nevertheless these measurements may be considered to demonstrate that, on an

[1] The standard errors of these percentage values were calculated by the formula $\frac{\sigma_x}{\bar{y}} = \sqrt{\frac{y^2 \cdot \sigma x^2 + x^2 \cdot \sigma y^2}{y^4}}$.

average, the three univalents are distinctly different in size, thus representing three different types of chromosomes. — Finally, it may be mentioned that clear size differences were also observed in four cells containing *four* univalents. The values obtained in these cells were the following: 4—4,5—6—7; 4,5—4,5—5—7; 4,5—5,5—6—6,5 and 5—5,5—6—6,5.

All the above measurements are based on slides from Fixation No. 387. To a smaller extent measurements were also effected with the aid of slides from the other fixation, No. 209. As previously mentioned, and as is evident from Table 7, the frequency of univalents is lower in this fixation. In 18 cells containing 2 univalents these were again found to be unequal in size but the differences were not so pronounced as in Fixation 387, the average size of the small univalents being 5,42 and that of the large ones 6,20. A calculation of the differences between the univalent pairs, in the same way as in Table 9, gave the average value 0,78, this value corresponding to 13,43 per cent of the average size (5,81). This percentage value is lower than the one obtained from Fixation 387 (25,96 $\pm$ 1,28), but in both fixations the size difference between the two univalents of the same cell is essentially greater than in the pure lines. As mentioned above, the size difference in the lines only amounted to 6,12 $\pm$ 0,75 per cent of the average univalent size.

D. CORRELATION BETWEEN POLLEN STERILITY AND MEIOTIC IRREGULARITIES.

According to Table 7 (p. 139), all the F_1 generations studied had a higher percentage of univalents at first metaphase than any of the pure lines. As the F_1 generations quite frequently have a reduced pollen fertility in comparison with the pure lines a direct causal relationship between partial sterility and occurrence of univalents might be suspected. Indeed, the presence of univalents should cause the formation of a certain percentage of gametes with a deviating chromosome number and in all probability such aneuploid gametes are less viable than the euploid gametes.

A comparison between the last two columns of Table 7 reveals, however, that there is no sure correlation between the frequency of univalents and the degree of pollen fertility characteristic of the F_1 combination in question. If the average values of the nine F_1 generations studied are arranged in a series according to an increasing percentage of univalents, the following pairs of values will be obtained: 18—67, 25—92, 26—69, 28—87, 39—87, 54—98, 60—55, 68—75, 69—71.

The first value in each pair represents the frequency of univalents, the second value the percentage of good pollen [1].

The absence or, at any rate, the very low degree of correlation between frequency of univalents and pollen fertility is, for instance, evident from a comparison between the F_1 combinations $B \times C$ (and reciprocally) and $B \times G$ (and reciprocally). The plants fixed of the former combination were markedly sterile (on an average 67 per cent good pollen), but meiosis was almost as regular as in a pure line, univalents only occurring in about 18 per cent of the cells. In the latter combination, on the contrary, the percentage of apparently good pollen, 75, was higher though the frequency of univalents was as high as 92 per cent in one of the fixations and 46 per cent in the other.

These data admit our drawing the definite conclusion that *the occurrence of univalents at meiosis and resultant irregularities is not the essential cause of the pollen sterility.* As will be further shown below, the truth is rather that pollen sterility and disturbed chromosome pairing are different symptoms of one and the same cause, *viz.* structural differences between the lines crossed.

V. CYTOLOGICAL INVESTIGATIONS IN GALEOPSIS SPECIOSA.

In the foregoing (pp. 131—135) a case of genotypically controlled sterility in *Galeopsis speciosa* was described. The main result of this investigation was the demonstration that certain progenies of partially sterile mother plants segregated in sterile and fertile daughter plants in about equal numbers, the progenies of fertile mother plants, on the contrary, only giving fertile progeny.

As is evident from a cytological examination of some sterile and fertile plants, the partial sterility in this species is also correlated with certain cytological disturbances. — In the first place the frequency of univalents was studied, the results of these observations being summarized in Table 10. Two fertile and three partially sterile mother plants were investigated. All of these belonged to segregating progenies and are thus the descendants of partially sterile mother plants.

---

[1] In order to make the comparison as exact as possible the pollen percentages represent the values obtained just from the fixed plants and not the average values given in Diagram 1. In most cases the differences between these values are rather slight.

The frequency of univalents in the fertile plants was very low. In one of the plants not a single univalent was observed among the 123 I—M groups examined, and in the other plant the percentage of metaphase groups with univalents amounted to 2,7 (average of three slides). Two of the three sterile plants also had a low, though slightly higher frequency of univalents (5—6 per cent) than the fertile plants. In the third plant, on the contrary, the univalents were rather numerous, occurring in 23 per cent of the cells. — The chromosome number in

TABLE 10. *The frequency of univalents in fertile and partially sterile plants of G. speciosa.*

Field-No.	Fix.-No.	Prep.-No.	Per cent of good pollen	Number of univalents outside the I—M groups 0	1	2	3	Number of I—M groups observed	Per cent of I—M groups with 1 or more univalents
34—188—1	206	1	93	115	—	5		120	4
»	»	2	»	142	—	3		145	2
»	»	3	»	105	1	1		107	2
34—188—1, total				362	1	9		372	2,7
34—188—14	217	1	96	123				123	0
35—137—14	406	1	56	101	4	2		107	6
34—187—3	215	1	46	185	3	6		194	5
»	»	2	»	62	2	2		66	6
34—187—3, total				247	5	8		260	5,0
34—186—3	213	1	57	83	12	12	1	108	23

speciosa being only half as high as in *Tetrahit*, a frequency of 23 per cent in this diploid species corresponds to the double value (46 per cent) in the tetraploid species. Thus, in comparison with *G. Tetrahit*, a univalent frequency of 23 per cent in *speciosa* must be considered to represent a rather considerable degree of irregularity.

A close study of meiosis in this plant revealed that the cytological irregularities were not only limited to an increased frequency of univalents but also involved the occurrence of *associations of four chromosomes* besides bivalents and univalents. The frequency of such quadrivalents is evident from the following survey of the different I—M configurations observed in this plant:

Configuration	*Side view*	*Polar view*	*Total*
8_{II}	18	4	22
$7_{II} + 2_{I}$	4	—	4
$1_{IV} + 6_{II}$	13	6	19
$1_{IV} + 5_{II} + 2_{I}$	4	3	7
$1_{III} + 6_{II} + 1_{I}$	3	—	3

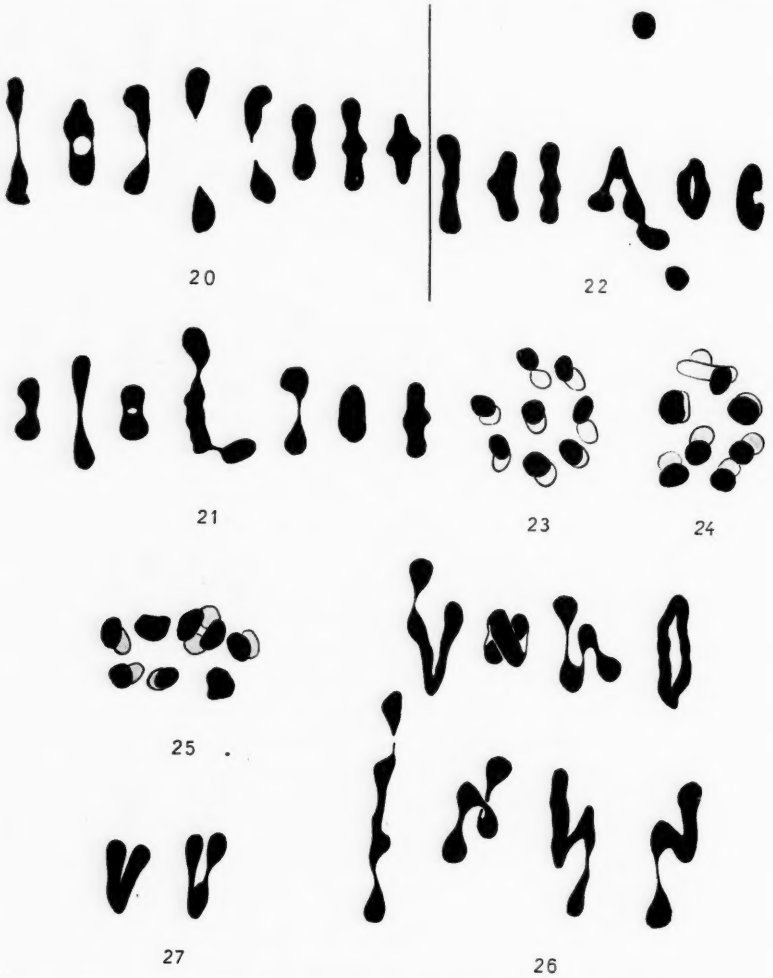
According to these values, quadrivalents (or trivalents) occur in 53 per cent of the cells. In reality, however, the frequency of cells with quadrivalents is probably somewhat higher. In several cells it could not be decided with certainty whether the metaphase groups contained quadrivalents, and such uncertain cases were not included in the survey of the configurations given above. Thus 15 additional cells probably or possibly contained $1_{IV} + 6_{II}$ and in two other cells the configurations were probably $1_{IV} + 5_{II} + 2_{I}$ and $1_{III} + 5_{II} + 3_{I}$ respectively. If these 17 values are also included in the counts, the average percentage of cells with quadrivalents will be raised from 53 to 64. Thus, at any rate, at least half of the metaphase groups of this plant contained a quadrivalent or, in a few cases, a trivalent and a univalent instead of the quadrivalent.

It should be observed that never more than *one* quadrivalent or trivalent occurred in the same cell. Thus, there is reason to consider the plant in question to be heterozygous for a segmental interchange between two non-homologous chromosomes. This interchange is obviously reciprocal, some of the quadrivalents appearing as closed rings, though the majority occur as zig-zag-shaped or straight chains. — Eight separate quadrivalents and two trivalents are represented in Figs. 26—27. The other figures show some complete metaphase groups with or without quadrivalents. In Figs. 20 and 23 the chromosome complement consists of 8_{II}. Figs. 21, 24 and 25 contain $1_{IV} + 6_{II}$ and in Fig. 22, finally, there are $1_{IV} + 5_{II} + 2_{I}$.

In contrast to the partially sterile plant described above one of the fertile plants (34—188—1, Table 10) showed no trace of multivalents at the I—M stage, and in other respects meiosis in this individual was also found to be quite regular. In 57 of 60 metaphase groups examined the chromosome complement consisted of 8_{II}, and in the 3 remaining cells there were $7_{II} + 2_{I}$.

According to these results, the cytological difference between fertile and partially sterile *speciosa* plants would appear to be perfectly clear. The situation, however, is evidently more complicated. If the partial sterility in this material is correlated with occurrence of quadrivalents,

cytological complications of the same type would be expected in all partially sterile individuals. However, an examination of the two other sterile plants (34—187—3 and 35—137—14, Table 10) showed meiosis



Figs. 20—27. I—M groups and multivalents in a partially sterile individual of *Galeopsis speciosa*. — Fig. 20, the most frequent configuration, 8_{II}; Fig. 21, $1_{IV} + 6_{II}$: Fig. 22, $1_{IV} + 5_{II} + 2_{I}$; Fig. 23, polar view with 8_{II}; Figs. 24—25, polar views with $1_{IV} + 6_{II}$; Fig. 26, 8 different quadrivalents from different groups; Fig. 27, 2 trivalents.

in these individuals to be very nearly regular. In the plant 34—187—3 8_{II} was observed in 46 cells, $7_{II} + 2_{I}$ in 3 cells and a trivalent was found in only one cell, this cell consequently containing $1_{III} + 6_{II} + 1_{I}$. In the other plant (35—137—14) 8_{II} was observed in 17 cells and $7_{II} + 2_{I}$ in one cell. The regular meiosis in these plants is reflected by a low frequency of univalents. According to Table 10 this frequency only amounted to 5—6 per cent, the plant with quadrivalents (34—186—3), on the contrary, having an essentially higher value (23 per cent).

The different mode of meiosis in these partially sterile individuals may be due to different causes. A first possibility is that the two plants having regular meiosis were sterile on account of incidental external influences, whereas sterility in the third plant was due to genotypical causes. As pointed out above, the segregation fertile : sterile is in this material often disturbed by environmental causes, different flowers of the same individual sometimes giving quite different pollen percentages. This possibility, however, is improbable, since the pollen fertility of all the sterile plants cytologically examined were tested 2 or 3 times with rather similar results. Thus, the plant 35—137—14 gave the values 53 and 58 per cent good pollen, the corresponding values from three slides of the plant 34—187—3 being 42, 44 and 53. The plant with quadrivalents (34—186—3), finally, gave the values 47 and 67. Thus, as regards the percentage of good pollen there was no significant difference between the plants, and consequently there is reason to believe that all three were genotypically sterile.

Another more plausible possibility is that the chiasma frequency, due to slight environmental changes, may be somewhat different in different plants, and that quadrivalents only occur in cells and plants having a relatively high total chiasma number. This possibility is supported by the fact that the formation of quadrivalents in the plant containing such associations was not complete, quadrivalents only occurring in about half of the cells. Whether this hypothesis is correct or not can only be decided by continued investigations. At any rate it is highly probable that the cytological complications are correlated with the partial sterility, and that this sterility is caused by heterozygosity for structural differences. Under certain conditions this heterozygosity also results in cytological complications. In the main, however, these complications as such do not cause a decreased fertility. As in *G. Tetrahit* sterility and deviating chromosome pairing are probably different symptoms of the same cause, *viz.* structural chromosome differences.

VI. DISCUSSION.

1. EVIDENCE THAT INTRASPECIFIC STERILITY IN GALEOPSIS IS DUE TO DIFFERENCES IN CHROMOSOME STRUCTURE.

A. INTRODUCTION.

The classical cases of intraspecific sterility, *e. g.* in the genera *Datura*, *Zea* and *Pisum* (cf. HÅKANSSON, 1931), are characterized by quite obvious cytological complications, *i. e.* the regular occurrence of chromosome rings or chains, consisting of four or more chromosomes. These cytological deviations are correlated with a certain degree of fertility reduction on the male as well as on the female side. In the most typical cases such plants are semi-sterile, having 50 per cent of aborted pollen grains and ovules, but stronger as well as weaker degrees of such sterility are also known, *e. g.* in *Zea* and *Pisum*.

With respect to degree and mode of inheritance the first cases of intraspecific sterility met with in *Galeopsis* were strikingly similar to the classical cases mentioned above. They deviated, however, so far as no cytological complications seemed to occur in the F_1 hybrids. Thus, in the paper of 1929 it was mentioned that, according to a preliminary investigation of meiosis in the $T—B \times T—C$ and $T—B \times T—X$ hybrids, no chromosome rings could be detected, meiosis also in other respects being apparently normal. In the paper of 1930 a it was mentioned that a markedly pollen sterile plant of the cross $T—B \times T—C$ not only had the normal chromosome number of 32 but also, as far as could be judged, a regular meiosis. In a later paper (1932 a), dealing with the same cross, it was again mentioned that the chromosome pairing was regular in several fertile as well as sterile F_3 plants. Two complete metaphase groups were represented, one from a fertile, the other one from a semi-sterile F_3 individual, both of them having 16 bivalents and showing no trace of ring or chain formation.

Thus, since no cytological complications could be detected in this cross in spite of the very marked sterility, and, further, since some other F_1 generations were found to be without rings or chains at meiosis, the conclusion was drawn that the same regularity was probably typical of all intraspecific *Galeopsis* hybrids. At the same time it was pointed out, however, that this absence of ring formation was no proof of the non-occurrence of translocations or segmental interchange. The ring formation might fail, if the segments exchanged were small and the chiasma frequency low (MÜNTZING, 1932 a, p. 102).

The cytological results described in the present paper confirm the

observation that meiosis in the $B \times C$ hybrids is very regular, and that there are no associations of four chromosomes. On the other hand, it has now been demonstrated that the univalent frequency in these hybrids is somewhat higher than in the parent lines and other pure lines. Thus, meiosis in this case is really slightly irregular, but to such a low degree that the disturbances could only be demonstrated by an accurate comparison with the pure lines. On the other hand, in the other F_1 combinations now examined the disturbances were generally more marked and in several cases quite striking. In view of these new results the conclusion may in fact be drawn that *also in Galeopsis intraspecific sterility is at least in part caused by structural differences between the lines crossed.* In the main this conclusion is based on the following three premises which will be considered in detail below:

1) Some F_1 combinations are characterized by the occurrence of certain definite I—M configurations, involving multi- and univalents. By reason of this feature these F_1 hybrids differ sharply from the pure lines, in which there are generally 16 bivalents.

2) In all the F_1 combinations examined the frequency of univalents is higher than in any of the pure lines.

3) If there are two or more univalents in the same metaphase group these univalents, at least in one particular F_1 combination, differ significantly in size. This is not the case in the pure lines.

B. DEFINITE CONFIGURATIONS IN THE F_1 HYBRIDS.

With respect to the I—M configurations the $D \times I$ hybrids represent the F_1 combination studied most closely so far. As mentioned above, the typical configuration in this case was $1_{III} + 14_{II} + 1_I$. In one of the two fixations examined this configuration was met with in 13 cells of 19, the remaining 6 cells representing five other configurations, four of which contained trivalents. Pairing was normal, *i. e.* with 16 bivalents, only in one cell of 19. In the other fixation, in which the univalent frequency was lower, 25 metaphase groups could be analysed, 12 of them representing the typical configuration, the other cells showing four other configurations. By adding the values of the two fixations, it will be found that 16_{II}, the configuration representing the normal condition in pure lines, was only observed in 20 per cent of the cells, the most typical configuration of this F_1, $1_{III} + 14_{II} + 1_I$, occurring in 57 per cent. The remaining cells (23 per cent) represented 7 other combinations, 6 of which contained trivalents or quadrivalents (or both).

Already from these observations it is obvious that the parent lines cannot be structurally identical, but matters are complicated by the fact that the species is tetraploid and the genomes of the probable parent species, *speciosa* and *pubescens*, are partially homologous (MÜNTZING, 1930 a, 1932 b). However, in spite of this homology tri- and tetravalents are only quite exceptionally met with in the pure lines. Consequently, the strong contrast between the mode of chromosome association in the pure lines and certain F_1 combinations must be due to some special cause. With respect to the $D \times I$ cross this cause must consist of structural differences between the lines. Since several other F_1 combinations behave in a similar way (cf. above, pp. 140—141) such structural differences between the different lines must be rather frequent.

The chromosome configurations in the different F_1 hybrids are as yet too little known to allow detailed conclusions being drawn as to the degree and kind of the structural differences. However, the formation of trivalents, which seems to be typical of several F_1 combinations, may be due to several different causes:

In the first place it might be a typical case of segmental interchange, which should induce an association of four chromosomes. The chiasma frequency is low, however, and in the pure lines, too, most of the bivalents at first metaphase are only associated by one terminal chiasma. Under such circumstances it is probable that the association of all four chromosomes to a quadrivalent only occurs in rare cases, the result more often being, for instance, a trivalent + a univalent. This explanation would fit in nicely with respect to the $D \times I$ hybrids. In this combination the typical configuration was indeed $1_{III} + 14_{II} + 1_{I}$, but in one of the fixations (203), in which the chiasma frequency must have been higher, several metaphase groups with quadrivalents were observed.

A second possibility of explaining the occurrence of trivalents is that in the main the structural differences are limited in such a way that one chromosome in one of the lines is partially homologous with two chromosomes of the other line. In the simplest case the remaining 29 chromosomes may form 14 bivalents and 1 univalent.

A third explanation may also be suggested, *viz.* that, primarily, the 32 chromosomes form $15_{II} + 2_{I}$, the two univalents not being capable of association on account of incomplete homology. Secondarily, since the species is tetraploid, one or both of the univalents may be associated with other chromosome pairs with which they are completely or parti-

ally homologous. Though the species must be considered to be allotetraploid, there is reason to assume, as pointed out above, that to a certain extent there are pairs of corresponding bivalents. Thus, the 16 chromosome pairs of a *Tetrahit* line might be designated by A_1—A_2, B_1—B_2, C_1—C_2, etc. We presume that in a certain F_1 combination the chromosomes corresponding to the A_2 pair are incompletely homologous and therefore as a rule incapable of forming a bivalent. Further, for the sake of simplicity, it may be assumed that one of the A_2 chromosomes is typical, the other one structurally changed. Of the two univalents thus formed, one, the typical A_2 chromosome, in want of a quite homologous partner, may associate instead with the two A_1 chromosomes. In that way a trivalent will be formed, in part due to a structural difference between the lines, in part due to the tetraploid constitution.

C. THE FREQUENCY OF UNIVALENTS.

Obviously, the higher frequency of univalents in the F_1 hybrids than in the pure lines is correlated with the deviating chromosome configurations, which are typical of certain F_1 combinations. If trivalents are frequent, this is evidently almost always correlated with a corresponding frequency of univalents, and inversely, if a certain F_1 combination is characterized by the presence of *one* univalent at the I—M stage (as is the case with several of the F_1 combinations in Table 7), it is highly probable that there is a simultaneous occurrence of one trivalent in the same metaphase groups. Thus, if an odd number of univalents is frequent in a certain F_1 type, this strongly indicates that the parent lines are not quite homologous with respect to the structure of the chromosomes.

In the hybrids between the *B* and *C* lines univalents were found to be present only in 18 per cent of the cells, and the occurrence of two univalents was more frequent than single univalents. Thus, this F_1 combination almost behaves like a pure line and only deviates by a slightly higher percentage of metaphases with univalents, the average values of the pure lines ranging from 0 to 12 per cent (Table 6). Further, cells with *one* univalent seem to be relatively more frequent in this hybrid than in the pure lines. Thus, even in this case, representing the most regular F_1 combination hitherto met with, there is reason to believe that structural differences between the parent lines influence the chromosome pairing. Thus, the simultaneous occurrence of two univalents must at least in part be considered to be the result

of non-conjunction in one or a few chromosome pairs in which the homology of the chromosomes is incomplete.

That a low but somewhat variable degree of non-conjunction occurs in the pure lines may be quite accidental or due to external disturbances of some kind, preventing the pairing in one or in rare cases in two chromosome pairs. It seems more plausible, however, that the univalents appear as a result of occasional interspecific pairing, *i. e.* conjugation between A_1 and A_2 instead of A_1—A_1 and A_2—A_2. Since the homology between A_1 and A_2 (respectively B_1 and B_2, etc.) may be incomplete, such exceptional chromosome pairs must have a more or less marked tendency to non-conjunction. This rather plausible hypothesis is supported to some extent by the fact that the frequency of univalents in the fertile *speciosa* plants was very low. In four slides from the two individuals hitherto examined the percentage of metaphases with univalents varied from 0 to 4. Even if these values are doubled in order to be comparable with *Tetrahit*, having the double chromosome number, the average value of *speciosa* will be as low as 4,0, the corresponding value of *Tetrahit* amounting to 8,6. Though this difference is based on too few values to be significant, it nevertheless indicates that the frequency of univalents is relatively higher in *Tetrahit*. This should be expected since the tetraploid species, in contrast to the diploid *speciosa*, has the opportunity of interspecific pairing.

D. UNIVALENTS OF DIFFERENT SIZE.

That the intraspecific sterility in *Tetrahit* is entirely or partly due to structural line differences is also evident from the univalent measurements in the $B \times G$ hybrids. In this F_1 combination the frequency of univalents was high, cells with 1—3 univalents being quite common, especially in one of the fixations (201, cf. Table 7). These univalents differed markedly in size, and in cells containing two univalents they were found to represent two distinct size classes. In the simplest case these two univalents might correspond to a chromosome pair, and in such a case the remaining 30 chromosomes should be united to 15 bivalents. Indeed, one of the few completely analysed metaphase groups of this F_1 combination probably consisted of $15_{II} + 2_I$ (cf. above, p. 141). In this case it is at once conceivable why these two univalents in most of the cells are not united to a bivalent. The chromosomes in question are unequal in size and thus structurally different. The smaller chromosome might of course be quite homologous with a corres-

ponding portion of the larger partner, but even in such a case the small size renders it liable to remain unpaired.

However, in this case the structural differences are certainly not only made up of a deficient homology in one of the chromosome pairs, but matters are more complicated. This is, for instance, rather evident from the fact that three of the four complete metaphase groups distinguished contained trivalents (cf. p. 141). Further, the number of univalents was often higher than two, and in cells with 3 univalents these univalents in all probability represented three different size classes. — From all these data it is quite evident that the occurrence of univalents in this F_1 combination is due to incomplete homology between the genomes of the parent lines and not to accidental non-conjunction between quite homologous chromosomes.

E. IS STERILITY A CONSEQUENCE OF INTERSPECIFIC PAIRING?

As mentioned above, the analysis of the intraspecific sterility in *Tetrahit* is complicated by the fact that the species is tetraploid and its genomes are partially homologous. Under such circumstances intraspecific sterility and deviating chromosome configurations in the F_1 hybrids might perhaps exclusively be secondary consequences of interspecific pairing, a possibility suggested by SANSOME and PHILP (1932, p. 307). Returning to the symbols used above, a typical line with the gametic constitution A_1—A_2, B_1—B_2, etc. might give rise to a new type with the constitution A_1—A_1 instead of A_1—A_2. — Crosses between the lines A_1—A_1 and A_1—A_2 would give F_1 hybrids with the zygotic constitution $\frac{A_1—A_1}{A_1—A_2}$. F_1 hybrids of this kind should have a tendency to form trivalents (A_1—A_1—A_1) + univalents (A_2) instead of two bivalents. There is also reason to assume that the fertility would be reduced on account of the presence of univalents and ensuing irregularities.

Since univalents as well as trivalents were found to be typical of several different F_1 combinations it might be considered whether the sterility phenomena and the deviating chromosome pairing should not be interpreted altogether in this way and not be regarded as due to segmental differences between certain chromosomes. Thus, the difference between the two explanations would consist in the assumption of rearrangements of entire chromosomes in the one case and of chromosome segments in the other. However, a more thorough consideration demonstrates that interspecific pairing and its consequences cannot be

the true or at least not the most essential cause of the sterility phenomena and cytological complications observed. The following circumstances argue definitely against this possibility:

a) It is probable that deviating gametes with the constitution A_1—A_1, instead of A_1—A_2, are more or less lethal, since they represent a disturbance of the balance, one chromosome from one of the gametes being absent and one chromosome of the other genome being duplicated. Even if such gametes are really functional it is probable that the resulting homozygous lines, having 4 A_1 chromosomes, will be less viable than normal lines with 2 A_1 and 2 A_2 chromosomes, and hence such lines would be eliminated by natural selection.

b) Lines with four completely homologous chromosomes should have a marked tendency to form quadrivalents. Not a single one of the lines hitherto studied has behaved in that way. At the I—M stage the chromosomes almost without exception are present as 16 bivalents. An exceptional quadrivalent was only observed in one single cell (Fig. 3).

c) According to the alternative hypothesis under discussion, the sterility should be due to the presence of univalents at I—M and their irregular distribution in the ensuing divisions. Under such circumstances F_1 combinations without univalents or with a low frequency of univalents should have good fertility, and a positive correlation should be expected between univalent frequency and degree of sterility. However, as demonstrated above (p. 150), this correlation is very weak or entirely absent. An extreme case is represented by the markedly sterile $B \times C$ hybrids, in which meiosis is almost quite regular. Sterility in hybrids of this kind must certainly be due to real structural differences between the parent lines and cannot be explained by the other hypothesis.

d) The conclusion that the chromosomal differences between the *Tetrahit* lines involve segmental interchange or other structural alterations is strongly supported by the fact that a clear case of segmental interchange has now been found in the diploid *speciosa*. Sterility in this *speciosa* material is evidently inherited in essentially the same way as in several *Tetrahit* crosses and is partly correlated with cytological complications, which must be interpreted as being the result of a reciprocal exchange of segments between non-homologous chromosomes. Since *speciosa* is diploid the other alternative explanation, discussed with respect to the tetraploid species *Tetrahit*, is entirely out of the question.

Consequently, the general conclusion to be drawn from the above

arguments is that intraspecific sterility in *Tetrahit* as well as in *speciosa* is entirely or mainly caused by structural chromosome differences. In addition to this essential cause of sterility it is possible that in certain cases sterility is due to or influenced by the fact that, as a result of interspecific pairing, the lines crossed differ with respect to entire chromosomes. From the rather strong arguments given above it is evident, however, that this possibility is not very plausible.

2. WHY ARE STRUCTURAL DIFFERENCES FREQUENT IN G. TETRAHIT?

As a result of the fertility investigations of the 66 F_1 combinations the conclusion could be drawn that, with respect to the causes of sterility, the 12 lines investigated belonged to no less than nine or ten different categories. According to the arguments just discussed, it may now be stated with certainty that, essentially, the sterility is caused by structural differences between the biotypes. Thus, it may further be concluded that *the pure lines constituting the species Galeopsis Tetrahit are very often structurally different.*

As pointed out above (pp. 127—129), it is impossible on morphological or plant-geographical grounds to predict whether two lines will react similarly or differently as regards sterility or fertility. In several cases lines from the same or neighbouring localities behaved differently and must therefore have a different structural constitution. Thus, in contrast to the conditions in *Datura*, in which structural differences are mainly found between races of widely different geographical origin (BERGNER and BLAKESLEE, 1932; BERGNER, SATINA and BLAKESLEE, 1933; BLAKESLEE, 1934), it may happen in *Galeopsis* that several and probably a great many structural types may be represented within a very limited sphere.

The most direct cause of this structural variation is probably spontaneous hybridization between *Tetrahit* and the related, also tetraploid, species *bifida*. Indeed, a large part of the material was derived from localities or geographical areas in which both the species grow together and form hybrids. As previously demonstrated in detail (MÜNTZING, 1930 a), there is reason to assume that the polymorphism of both the species is essentially caused by the fact that they frequently intercross in nature. In previous papers on intraspecific sterility in *G. Tetrahit* (MÜNTZING, 1929, 1930 a, 1932 a) the hypothesis was advanced that the causes of sterility must be connected with the fact that all *Tetrahit* lines are the more or less remote descendants of *Tetrahit* $\times$

bifida hybrids. For that reason the *Tetrahit* lines will sometimes contain chromosomes or genes of the other species, this being the cause of sterility in certain crosses. Now since it has been proved that the causes of sterility are structural differences, there is reason to examine whether such differences may arise in *Tetrahit* × *bifida* hybrids.

Meiosis in such F_1 hybrids has been subject to a preliminary study (MÜNTZING, 1930 a) but direct observations demonstrating the origin of structural differences have not yet been made. However, investigations of other species hybrids go to show that species hybridization may be an important cause of new structural alterations. One of the first examples of this kind was found in *Vicia* by SWESHNIKOWA (1932). In the progeny of species hybrids in *Crepis*, NAVASHIN (1934) observed new chromosome types not present in the parent species. Similar, though not quite definite, observations were made by BABCOCK and EMSWELLER (1936) with respect to the cross *Crepis nicœensis* × *setosa*. According to my own experience from the same genus, *viz.* the hybrid *C. dioscoridis* × *divaricata* (MÜNTZING, 1934), a multitude of deviating chromosome types may be formed as a consequence of crossing-over between homologous segments with a different position in the conjugating chromosomes. Already this crossing-over process may give rise to many new, structurally different chromosomes, and a still greater number may be formed by later meiotic irregularities, such as fragmentation of double attachment chromosomes, etc. Such processes are probably rather frequent in species hybrids, though they have largely escaped attention. However, a good example of this kind has recently been described by LEVAN (1936). In the pollen divisions of the hybrid *Allium cepa* × *fistulosum* a number of new chromosome types were observed, which must have arisen as the result of »unequal» crossing-over.

A necessary condition for the formation of structural novelties during meiosis is that the chromosomes of the species crossed already are more or less different in structure. These primary differences may have arisen spontaneously or as a consequence of environmental influences of various kinds, *e. g.* changes in temperature or humidity. If such differences are combined in a hybrid, a large number of secondary structural changes may evidently arise all at once. Thus, though this needs to be verified, there is reason to assume that the multitude of structural types in *G. Tetrahit* is closely connected with the frequent natural hybridization between *Tetrahit* and *bifida*. Crosses between

structurally different biotypes within *Tetrahit* will certainly have a similar though less pronounced effect.

3. THE DEGREE AND FREQUENCY OF INTRASPECIFIC STERILITY IN GALEOPSIS.

Of the 66 F_1 combinations in *G. Tetrahit* only 30 had at least 90 per cent good pollen, the other 36 combinations representing lower values and thus a more or less pronounced sterility. However, the limit between fertile and sterile combinations is not sharply defined, and already for that reason it is doubtful whether all F_1 types with 90—100 per cent apparently good pollen are really as fertile as the parent lines.

Another indication that this is not the case is represented in Table 4 (p. 131), showing the correlation between reaction ratio and pollen fertility. According to this table, line pairs, reacting equally in 9 or 10 cases out of 10, gave F_1 hybrids with a higher pollen fertility than the line pairs representing the next lower class (equal in 7 or 8 cases out of 10). In the former class all the 6 F_1 combinations lie between 95 and 100, the average value being 97,5. In the second class fertility varies between 75 and 100 and is on an average 92,5. The somewhat lower fertility in this latter class is in excellent accordance with the fact that, judging from their mode of reaction with the other lines, the line pairs falling under this category are not quite homologous. Thus, it is probable that these lines are unequal in respect to slight structural differences, which in part cause a scarcely noticeable decrease in the percentage of morphologically good pollen in the F_1 hybrids and in part are evident by a somewhat different mode of reaction with other lines. That this slight decrease in fertility is really significant and not only accidental is strongly supported by the other values in Table 4. The more differently two lines react in crosses with other lines, the more sterile are evidently the lines in crosses with each other. This correlation is reflected by a quite continuous decrease of the average values from 97,5 to 65,8 (Table 4).

Judging from this table *probably only such lines as react identically in crosses with all other lines are quite fertile with each other.* In the present material it has only been possible to test the similarity of reaction with respect to 10 other lines. It is possible that this number is insufficient, and that two lines which have reacted in the same way with 10 other lines might nevertheless reveal significant differences, when crossed to a still larger number of biotypes.

A difficulty in exactly estimating the degree of fertility is the fact that the percentage of morphologically good pollen only represents a maximum value. In cases of slight sterility in particular it is certainly to be suspected that part of the apparently good pollen is not functional. This is exceedingly probable in such F_1 combinations as, for instance, $E \times G$ and $F \times G$, in which the percentage of good pollen was as high as 87 and 98, though (according to Table 7) the univalent frequency in

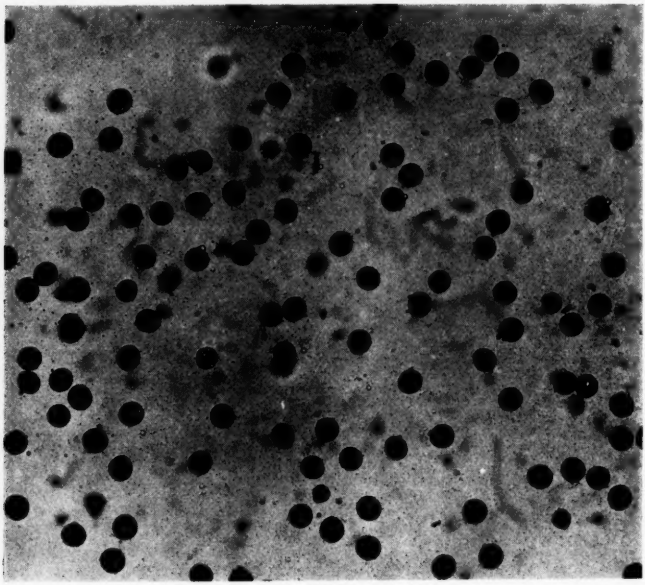


Fig. 28. Fertile pollen of the *Tetrahit* line *B*. (The pollen in this and the following figure mounted in a mixture of aceto-carmine and glycerin).

the same *plants* was found to be considerable and amounting to 39 and 54 per cent respectively. It is true, indeed, that pollen percentage as well as univalent frequency may be modified rather easily and, thus, the absence of a negative correlation between the values might depend upon the fact that the pollen samples and the fixations were made on different days. It should be observed, however, that the pollen percentage values found in the fixed individuals (87 and 98) were rather typical of these F_1 combinations in general, the average values of $E \times G$ and $F \times G$ being 88 and 92 (Diagram 1).

The relatively high frequency of univalents in these F_1 combina-

tions should by itself cause some decrease in fertility. Above all, however, the occurrence of univalents indicates structural differences between the parents, which should lead to the formation of lethal recombination gametes. Under such circumstances, and since the percentage of apparently bad pollen grains was low, it must be assumed that in these cases the lethal effect of the structural differences and meiotic irregularities is not very pronounced, the non-functional pollen

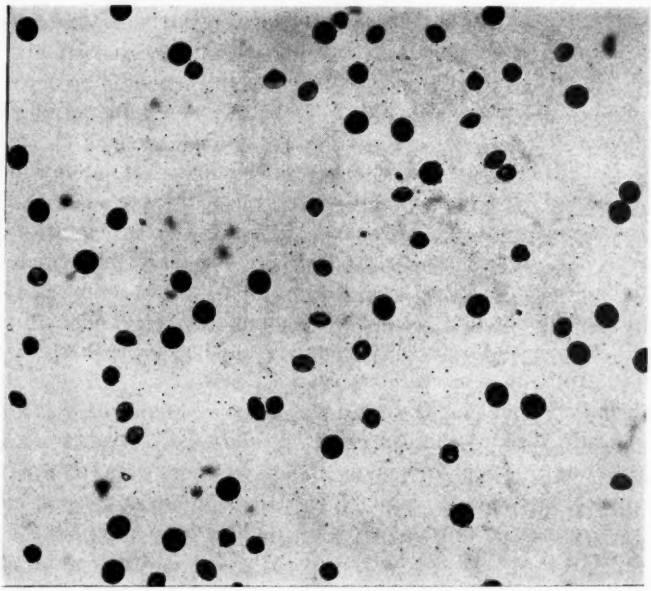


Fig. 29. Partially sterile pollen of the intraspecific *Tetrahit* hybrid $B \times C$.

grains being morphologically good but physiologically poor. Such »inactive» pollen grains are indeed known in several other genera.

To some extent this explanation is contradicted by germination experiments with the pollen of different F_1 combinations. In these cases, described in a previous paper (MÜNTZING, 1929, p. 307), the morphologically good pollen of three F_1 hybrids ($B \times X$, $A \times X$ and $A \times C$) was found to germinate just as well as the pollen of the parent lines. In contrast to the cases discussed above ($E \times G$ and $F \times G$), all these F_1 combinations have a more or less high percentage of morphologically poor and quite shrivelled pollen grains. It is probable that this quite

lethal pollen also represents all physiologically poor pollen classes. In the more fertile F_1 combinations, on the contrary, the limit between »good» and »poor» pollen grains is probably less distinct.

As pointed out above, there is no direct causal relation between pollen sterility and the occurrence of univalents at meiosis. Both these phenomena must rather be considered as different symptoms of the same cause, *viz.* structural differences between the lines crossed. However, even in such a case a certain parallelism between the degree of pollen sterility and the degree of cytological disturbances might be expected, if these phenomena are both proportional to the size and number of the structural differences. Since this correlation is entirely absent or at least very weak, this must be due to qualitative differences between the different chromosome segments. In such an F_1 combination as $B \times C$, in which sterility is strong but meiosis almost normal, there is reason to assume that the structural differences are small in quantity but qualitatively important. In other F_1 combinations, on the contrary, meiosis may be disturbed by rather large segmental differences, comprising parts of the chromosomes which, however, are relatively harmless to the viability of the gametes. — Though this interpretation is somewhat speculative, it probably represents the most plausible explanation of the observations made.

The main points in this chapter may be summarized as follows:

As a rule pure lines in *Galeopsis Tetrahit* have a structurally different constitution. On that account the F_1 hybrids are seldom as fertile as the parent lines but generally represent different degrees of sterility, ranging from rather extreme cases to combinations in which the fertility reduction is very slight and difficult to demonstrate. The absence of a correlation between univalent frequency and degree of pollen sterility must be due to qualitative differences between different chromosome segments.

4. CYTOLOGICAL DISTURBANCES AND INTRASPECIFIC STERILITY IN SOME OTHER GENERA.

A. DIFFERENT DEGREES OF STRUCTURAL ALTERATIONS AND THEIR EFFECTS.

The results in *Galeopsis* raise the question as to the extent in which similar phenomena occur in other genera. Thus, how frequent is intraspecific sterility, and is this sterility always accompanied by cytological complications? An exhaustive answer to these questions would lead

too far, but the problem may be illustrated by some characteristic examples. In this connection the discussion will, of course, be limited to such cases in which the parent types have the same number of chromosomes.

As already pointed out, the first typical cases of intraspecific sterility in *Datura*, *Zea* and *Pisum* were characterized by semi-sterility on the male as well as on the female side. This sterility is accompanied by marked and regular cytological deviations, four chromosomes being associated with each other to a ring-shaped configuration during prophase and metaphase. Several other equally pronounced cases have later on been observed in other genera.

Besides this typical category of intraspecific sterility, which is caused by segmental interchange between non-homologous chromosomes, it may happen, in other cases, that the sterility is weaker and the cytological phenomena less striking. With respect to sterility, hybrids with only 25 per cent bad pollen have been observed in *Datura* (BLAKESLEE, 1928) as well as in *Zea* (cf. CLARKE and ANDERSON, 1935, p. 715). This is considered to imply that only one of the two recombination gametes aborts visibly. In principle the same explanation was also given for the quarter-sterile *Galeopsis* hybrids (MÜNTZING, 1930 a, p. 226).

As is evident from the investigations in maize, the typical closed ring of four chromosomes may in certain cases be replaced by an open chain (BURNHAM, 1932; BRINK and COOPER, 1932), and in still other cases the multiple association is not formed at all but is replaced, in part of the cells, by two bivalents (CLARKE and ANDERSON, 1935). Earlier the open chains were considered to result from simple translocations, but according to later investigations (cf. CLARKE and ANDERSON, 1935) the segmental interchange is always reciprocal. However, the cytological effect of these reciprocal exchanges will be different according to the size of the segments involved. If both the segments are large, the result will be ring formation, if one segment is large, the other small, open chains are obtained and, finally, if both segments are small, two separate bivalents are often formed.

In connection with the results in *Galeopsis* the latter type is especially interesting. According to CLARKE and ANDERSON (l. c.), the segmental interchange in their material involved the replacement of about 25 per cent of the shorter arm of the »*a-ts*$_4$»-chromosome by part of the satellite (2 chromomeres) of the satellite chromosome. By studies of the pachytene configurations, which are exceedingly clear in maize,

it was possible in fact to demonstrate accurately that the segmental interchange was exactly of this kind. At diakinesis the four chromosomes were associated as two separate bivalents in 69 per cent of the cells and as an open chain in the remaining cells (31 per cent).

Thus, we have here a completely clear case, in which the segments exchanged are so small that cytological disturbances are only induced in a minority of the cells. In spite of this the segmental interchange also in this case causes an obvious decrease in fertility (l. c. p. 714). In some of the plants about half of the pollen was normal, the other half consisting of empty or only partly filled grains. In other plants of the same type only $^1/_4$ of the pollen grains were visibly aborted, the other $^3/_4$ being well filled but of variable size. Thus, plants of this kind are not typically semi-sterile but have somewhat better fertility. This fact is in excellent accordance with the continuous series of sterility degrees found in *Galeopsis*.

It might be objected, perhaps, that the maize material studied by CLARKE and ANDERSON was obtained after X-ray treatment, and that the products thus obtained are not comparable to spontaneous material. Other similar cases in wild plants are known, however, in which the occurrence of associations of four chromosomes in part of the cells indicates that the individuals in question are heterozygous for a segmental interchange, involving relatively small segments. Besides the size of the chromosome parts, the chiasma frequency typical of the species must also influence the degree of multivalent occurrence.

A typical case of this kind was observed in the diploid, wild species *Dactylis Aschersoniana* (MÜNTZING, 1937 b, pp. 116—122). A certain individual, collected in nature, was found to be partially sterile with an average of 47 per cent good pollen. At meiosis the chromosome configurations consisted of 7 bivalents in 55 per cent of the cells. The next category in frequency (38 per cent) showed 1 quadrivalent + 5 bivalents, whereas the remaining cells (7 per cent) mainly contained the configurations $1_{III} + 5_{II} + 1_{I}$ and $6_{II} + 2_{I}$. Of the quadrivalents, or more correctly, the associations of four chromosomes, the majority (87 per cent) were chain-shaped but the rest (13 per cent) were closed rings, thus demonstrating that also in this case the segmental interchange was reciprocal. Further, a closer study of the chiasma frequency revealed that, in the cases when the four chromosomes involved in the interchange appeared as two bivalents, the average chiasma number in these bivalents was in all probability lower than in the normal bivalents. By analogy with several other similar cases (cf.

DARLINGTON, 1931; LEVAN, 1936) this must depend on the fact that the chromosomes in these bivalents are not quite homologous but separated by minor structural differences.

Evidently, this *Dactylis* type behaves in the same way as the semi-sterile plant of *Galeopsis speciosa* described above (pp. 151—155). In this individual somewhat more than half of the pollen mother cells contained an association of four chromosomes. These quadrivalents were mainly chain-shaped but closed rings also occurred.

In the typical cases of semi-sterility the reduction of fertility is as great in the ovules as in the pollen. In *Galeopsis*, on the other hand, sterility was generally found to be more pronounced in the pollen than on the female side (MÜNTZING, 1930 a, 1932 a). Similar cases are also known in *Zea*. According to RHOADES and MCCLINTOCK (1935), BURNHAM has observed a case of segmental interchange characterized by viable female gametes but partially sterile pollen. In this case the exchange involved one large and one small segment.

From the examples given above it is quite clear that *in addition to the very marked and consequently first observed cases of intra-specific sterility there is another category, in which the sterility as well as the cytological complications are less prominent.* In all these cases, however, it is a question of segmental interchanges between non-homologous chromosomes. The effects of these structural alterations will largely depend upon the absolute and relative size of the segments exchanged and upon the chiasma frequency of the species in question. Further, the degree of sterility will certainly be influenced largely by the quality of the genes present in the segments exchanged. On an average, however, the genetical and cytological effects of the structural changes will be proportional to their quantity. Since, further, the effects of small changes of this kind are difficult to demonstrate, it is highly probable that slight structural differences are much more frequent than there has hitherto been reason to assume.

B. STADLER'S INVESTIGATIONS OF INDUCED MUTATIONS.

The view concerning the frequent occurrence of small structural differences is based especially on the very thorough investigations in maize and is in excellent agreement with the *Galeopsis* results described in the present paper. This theory finds further support in STADLER's investigations of experimentally induced mutations and their nature (STADLER, 1932, 1933). As is well known, X-ray treatment partly results in a lot of obvious chromosome aberrations, partly in alterations

which give the impression of being typical mutations. On the basis of his experience from such experiments in maize STADLER points out that there is evidently a large category of changes, which are intermediate between ordinary mutations and typical chromosome aberrations.

It is typical of gene mutations that they are transmitted without disturbances through the female as well as the male gametes, the chromosome aberrations, on the contrary, being accompanied by a marked sterility. The intermediate category is characterized by a partial elimination of the gametophytes, the fertility in such cases generally being higher on the female side than in the pollen. — In a special case of this kind it could be demonstrated that the structural change consisted of a typical but quantitatively rather small deficiency. This could be definitely shown thanks to the pachytene technique available in maize. In another plant species it would probably have been impossible to demonstrate the occurrence of this slight cytological alteration. This structural change, however, was sufficient to bring about a quite obvious decrease in fertility, which was greater in the pollen than in the ovules. The similarity to the conditions in *Galeopsis* is evidently striking, and this further strengthens the conclusion, previously drawn from other premises, that the frequent occurrence of intraspecific sterility in *G. Tetrahit* is due to small structural differences between the lines.

In a certain particular this similarity is so striking that it deserves special consideration. In the case, specially studied by STADLER (1933), in which certain pollen sterile plants were heterozygous for a small deficiency, there was a characteristic external difference between these heterozygotes and the homozygous, normal and fertile plants. The heterozygous plants were well developed but reached the flowering stage 2—4 days later than the normal plants. Further, when full-grown the homozygotes were found to be 6—12 inches taller than the heterozygotes. Thus, there was a rather weak but nevertheless clearly noticeable lethal effect also on the sporophyte generation.

A quite analogous effect was observed in *Galeopsis* in the cross between the *Tetrahit* lines *B* and *C*. As previously reported in detail (MÜNTZING, 1932 a, pp. 91—93), the partially sterile individuals in certain progenies were observed to reach the flowering stage much later than the fertile plants. These sterile plants originate from the union of one normal male and a sublethal female gamete. The latter is completely lethal in the pollen but is to a certain extent transmitted by the ovules. Therefore, the plants in question are probably heterozygous for a duplication or a deficiency. This disturbance of the balance causes

partial sterility but evidently also influences the sporophyte generation. Just as in *Zea*, this is expressed by a retarded growth.

C. INCREASED UNIVALENT FREQUENCY AS EVIDENCE OF STRUCTURAL DIFFERENCES.

As is evident from the preceding discussion there are continuous transitions between relatively large structural alterations, regularly causing multiple associations at meiosis, to small differences, which do not at all or only exceptionally influence the chromosome pairing visibly. In maize, thanks to the pachytene technique, it is nevertheless possible in such cases to prove that it is really a question of structural changes. In other organisms, in which this technique cannot be employed, the question is more difficult to solve. However, a last criterium remains, *viz.* the frequency of univalents, and if this frequency is high it is a strong indication of the presence of structural differences.

It is true, indeed, that chromosome pairing may be disturbed or quite inhibited by the action of single, specific genes. In such cases as in *Galeopsis*, in which the univalent frequency is generally higher in the F_1 hybrids than in the parent lines, it is perfectly clear, however, that the higher frequency of univalents is caused by differences in chromosome structure. As already pointed out, these differences will in the first place cause a decrease of the chiasma frequency, this in its turn causing a more or less marked tendency to incomplete chromosome pairing.

The occurrence of unpaired chromosomes in F_1 is very characteristic of many species hybrids but an almost unknown phenomenon in intraspecific hybrids. However, disturbances of this kind have been observed in a few cases. — In *Viola*, CLAUSEN (1926) found the chromosome pairing in F_1 hybrids between two biotypes of *V. arvensis* to be incomplete, the chromosome complement sometimes consisting of $15_{II} + 4_{I}$ instead of 17_{II}. In the following generations this incomplete pairing gave rise to aberrants with deviating chromosome numbers. As pointed out by the author (l. c. p. 53), it is in this case strange to find such a decrease in »affinity», the parental biotypes being of a very similar origin. As a possible explanation the author suggests that, on account of hybridization with the related species *V. tricolor*, one of the parental biotypes had obtained some deviating chromosomes from that species.

These conditions are rather similar to the *Galeopsis* crosses but with the difference that no sterility was observed in the *Viola* hybrid.

Nevertheless, it is probable that in *Viola*, as in *Galeopsis*, the lines are structurally different, and that the origin of such alterations in *Viola* is favoured by spontaneous hybridization between *tricolor* and *arvensis*. This conclusion is supported by the fact that several other *Viola* species are structurally different, judging from the multiple chromosome configurations which are typical of their F_1 hybrids (CLAUSEN, 1931).

Very interesting cases of increased univalent frequency have been observed by several authors in intra- and interspecific *Triticum* hybrids. The species hybrids in question represent combinations within the same chromosomal group and behave in essentially the same way as the strictly intraspecific combinations. Therefore, the inter- and intraspecific crosses may in this case be discussed together.

THOMPSON and ROBERTSON (1930) observed that the univalent frequency in hybrids between different species in the *vulgare* group was considerably higher than in the parent species. Thus, in the pure species, *vulgare*, *Spelta* and *compactum*, the percentage of cells with univalents varied from 4,0 to 4,4, the corresponding values of the three F_1 combinations possible being 42,0, 34,8 and 12,5 per cent. As to the possible causes of this increased frequency the authors suggest two alternative explanations. In the first place the parent types might differ with respect to entire chromosomes, *Triticum vulgare*, according to WINGE's theory, corresponding to the formula *ABC*, *Spelta* being *ABB* and *compactum ACC*. — As a second alternative it is supposed that the higher univalent frequency in the hybrids depends upon a more general decrease of affinity not limited to special chromosomes. This decrease is supposed to be due to »genetic diversity», a conception which in this connection probably implies small structural differences.

The latter explanation is supported by the fact that exactly the same phenomenon was observed in the tetraploid emmer group. In this case the univalent frequency of the pure lines varied between 0,5 and 3,5 and in the hybrids between 1,8 and 26,9. All twelve hybrid combinations examined had a higher univalent frequency than the parent species. Similar observations were also made by VAKAR (1932).

Further information about the chromosome conditions in the emmer group has been furnished in a detailed paper by HOSONO (1935). HOSONO has not only determined the univalent frequency but also made out the complete chromosome configurations in a large number of pollen mother cells in hybrids as well as in pure species. The main result of these investigations is the following: Though different hybrid combinations behave differently, the hybrids, on an average, have a

more irregular meiosis than the parent species. This may in part manifest itself as an increased frequency of univalents but is especially apparent in the shape of associations of four chromosomes. Very often the chromosome configurations in the hybrids consist of $1_{IV} + 12_{II}$, more rarely there are two quadrivalents ($2_{IV} + 10_{II}$).

The occurrence of such quadrivalents might possibly depend upon partial homology between the *A* and *B* genomes of the emmer group and thus be a sequel of the tetraploid constitution. This, however, cannot be the essential cause, since quadrivalents are almost quite absent in the parent species. Under such circumstances the associations of four chromosomes must be mainly caused by structural differences between the parents, a conclusion which is also, though with hesitation, drawn by HOSONO.

The correctness of this conclusion, however, is verified by the following circumstances: Firstly, the »quadrivalents» are often chain-shaped and not closed. Since the chiasma frequency in *Triticum* is rather high this indicates that the chromosomes are not completely homologous. Further, HOSONO observed that fixations of the same material in different days may give rather different results with regard to the type of chromosome association [1]. In this connection it was noticed that there was an inverse proportionality between frequency of univalents and quadrivalents. Thus, if the frequency of quadrivalents is low, the number of univalents is high. In fact, if the quadrivalents consisted of homologous chromosomes, they should in such cases be replaced by two bivalents rather than by univalents.

Thus, the cytological results demonstrate that in this material the parent types are often distinguished by structural chromosome differences. This being the case, the F_1 combinations should be partially sterile. However, an investigation of the seed setting after open pollination seems to indicate that most of the F_1 combinations are as fertile as the pure species (HOSONO. l. c.). This is unexpected but may in part be explained by the fact that all emmer species must be considered to be partially autotetraploid. As mentioned above, the *A* and *B* genomes of these species are partially homologous. Since autopolyploidy generally diminishes the susceptibility to disturbances of the balance (cf. MÜNTZING, 1937 b), it is quite likely that gametes with small duplications or deficiencies are viable, especially the female ones. As emphasized above, fertility is generally better in the ovules than in the

[1] As previously mentioned, this is also characteristic of the *Galeopsis* material (cf. Table 7, and the discussion, pp. 139—144).

pollen, especially in the case of sterility caused by slight structural differences. The emmer hybrids under discussion have not been examined with respect to the pollen fertility. Judging from the conditions in *Galeopsis*, it is rather likely that even in these hybrids the pollen will be less good than in the homozygous parent types.

The cases in *Triticum* hitherto discussed have all consisted of crosses between relatively widely separated types in the *vulgare* and emmer groups respectively. However, cytological disturbances have also been observed in strictly intraspecific wheat hybrids. HOLLINGSHEAD (1932) studied the chromosome pairing in a number of varieties and their hybrids in *Triticum vulgare* and *T. dicoccum*. In both these species the F_1 hybrids had, on an average, a higher frequency of univalents than the parent types. In five *vulgare* varieties the percentage of cells with univalents was found to vary between 2,9 and 9,7, the corresponding figures of ten F_1 combinations ranging from 5,2 to 39,1. Seven of these ten combinations had a higher univalent frequency than either of the parent varieties. In the same way a hybrid between two *dicoccum* varieties showed such a high frequency of univalents as 24,5 per cent.

Thus, it is quite evident that plainly noticeable cytological disturbances are common in F_1 hybrids in *T. vulgare* and other wheat species. As in the cases studied by HOLLINGSHEAD, this may happen even if the parent lines are rather closely related. Just as in the intraspecific *Galeopsis* hybrids, the disturbances chiefly consist in an increased rate of cells with univalents. In wheat, these disturbances have not been observed to be correlated with intraspecific sterility, but no investigations of this kind have been undertaken, however, at least not with respect to the pollen. HOLLINGSHEAD (l. c.) does not give any explanation of the higher frequency of univalents in the hybrids but simply regards it as »an exaggeration of a condition occurring in varieties . . .». Considering the other investigations in wheat, especially HOSONO's new results (HOSONO, 1935), it is now fairly certain that also in these cases the cytological disturbances are caused by small structural differences between the parent types. This opinion is, indeed, supported by the observation made by HOLLINGSHEAD (1932) that the hybrids had not only an increased frequency of univalents but also a lower chiasma number in the bivalents. This fact also indicates that the parent types were structurally different.

D. A THEORY CONCERNING THE CONNECTION BETWEEN THE OCCURRENCE OF FREQUENT STRUCTURAL DIFFERENCES AND THE INBREEDING PHENOMENA.

Spontaneous intraspecific differences in chromosome structure are now known from a rather large number of plant genera. In the preceding chapters such cases, in addition to *Galeopsis*, were mentioned to occur in *Datura*, *Zea*, *Pisum*, *Triticum* and *Dactylis*. Many other similar cases have been described, for instance, in *Vicia* (SWESHNIKOWA, 1929), *Campanula* (GAIRDNER and DARLINGTON, 1930), *Rosa* (ERLANSON, 1933), *Secale* (DARLINGTON, 1933), *Festuca* and *Alopecurus* (RANCKEN, 1934), *Tradescantia* (ANDERSON and SAX, 1936) and *Paris* (GEITLER, 1937). Some further examples are cited by DARLINGTON (1937, p. 274).

In the self-fertilizing species it is in such cases a question of differences between pure lines, which become apparent only after intraspecific hybridization. In the cross-fertilizers, on the other hand, single individuals have been directly observed to be heterozygous for one or more structural differences, which are transmitted to the progeny in a regular way. Thus, structural intraspecific differences are known in self- as well as cross-fertilizers and everything indicates that such differences are quite frequent in plant species.

Judging from some recent results the same thing probably holds true also of animal species. Thanks to the salivary gland technique a large number of induced as well as spontaneous structural changes have been analysed in *Drosophila*. Of most interest in this connection is the analysis of wild populations. DUBININ, HEPTNER, DEMIDOVA and DJACHKOVA (1936) studied the genetic composition of a Russian population of *Drosophila melanogaster*. Among a total of 1400 mutations, observed by these authors, there were 218 lethals and 68 inversions. Inversions in rather high concentrations were also found in the various populations of different *Drosophila* species and *Chironomidæ* studied by DUBININ, SOKOLOV and TINIAKOV (1936). The group *Chironomidæ* has also been subject to detailed investigations by BAUER (1936). This author also finds inversions to be most frequent, but other chromosome aberrations were also met with. A very similar situation was again met with in the grasshoppers *Chorthippus* and *Stauroderus* (DARLINGTON, 1936). Further literature on differences in chromosome structure within animal species is summarized by BAUER (1937, in the press).

The most striking feature in these new reports is the high frequency of inversions and the low frequency or complete absence of other structural changes. A rather similar situation is also characteristic

of at least one botanical object, *Paris quadrifolia* (GEITLER, 1937). This predominance of the inversions may in part be due to a higher selection value but perhaps also to the greater difficulty of demonstrating the occurrence of certain other structural changes, *e. g.* small deficiencies. This suspicion is strengthened by results recently obtained by DEMEREC (1937). With the aid of salivary gland studies this author was able to demonstrate that quite a number of lethals in *Drosophila melanogaster* without exception represented small deficiencies.

Thus, there is ample evidence of a rather frequent occurrence of chromosomal aberrations in plants as well as in animals. The same thing probably occurs also in *Homo*. KOLLER (1937) has recently reported the probable occurrence of an inversion in Man. — It is of course natural that if the structural alterations are small their real nature is difficult to demonstrate. Therefore, the relatively gross alterations have in the first place been observed, but it is now quite clear that there is another category of smaller structure differences, having a less drastic effect. According to the previous argumentation and my own results in *Galeopsis,* there is good reason to assume that this category is very comprehensive. The transitions between large and small structural differences seem to be quite continuous and it is also rather difficult to decide the position of the lower limit, *i. e.* the limit between structural differences and true gene differences. By future investigations it may perhaps be possible to demonstrate that most of the biotypes in a self-fertilizing species are structurally different, just as most of the individuals in a cross-breeding population.

Already now it is evident, however, that intraspecific differences in chromosome structure are much more frequent than has hitherto been generally assumed. This fact in itself is of interest but will probably also be attended by consequences to certain general problems of genetics, such as the species question, the problems of inbreeding degeneration and self-sterility, etc. In the present connection the discussion will be limited to some considerations of the inbreeding phenomena.

If my assumption should prove to be correct that structural differences are frequent among the individuals of a cross-fertilizing population, such a condition would be in excellent accordance with the general occurrence of inbreeding degeneration after selfing. This depression may, indeed, be caused by several different factors (cf. HERIBERT NILSSON, 1937), but all workers probably agree, that it is essentially due to the segregation of unfavourable or even more or less lethal recessive factors. If the structural differences consist of different

deficiencies, duplications, etc. it is conceivable that individuals and strains which become homozygous for these alterations will acquire a more or less reduced viability and reach their inbreeding minima at different levels. This conclusion does not involve any really new point of view, it only calls attention to the fact that the factors depressing viability often, perhaps always, consist of structural deviations. Another conclusion, however, is perhaps of greater interest, *viz.* that in all probability these structural influences will also influence the gametophytes, at least on the male side. In addition to real partial sterility this should also in many cases induce differential pollen tube growth and in this way selective fertilization. Since the classical cases in *Oenothera* and *Melandrium* certation phenomena have been observed in several other plant genera.

In this connection the detailed investigations on pollen tube growth in certain chromosomal aberrants of *Datura stramonium* are of special interest. In a paper by BUCHHOLZ and BLAKESLEE (1930) a report is given of the pollen tube growth in a 2n + 1 form, »Rolled», and its two secondaries, »Sugarloaf» and »Polycarpic». Pollen grains with these three kinds of chromosomes behave in the following way when placed on an ordinary 2n stigma: Pollen grains containing the »Rolled» chromosome germinate satisfactorily, but the pollen tubes swell and burst in the style after a short period of growth. One of the two types of secondaries (»Polycarpic») inhibits germination completely, and pollen grains carrying this chromosome thus fail at the very start. The other secondary type, on the other hand, facilitates germination as well as pollen tube growth and fertilization and, thus, extra chromosomes of this type may be transmitted through the pollen. However, the rate of pollen tube growth in this case is considerably lower than in normal plants.

These results strikingly demonstrate that different segments in the same chromosome may have quite different effects on pollen tube growth. If the quantity of one of the segments is increased, it will have a very deleterious effect and will prevent pollen tube growth entirely. Thus, such grains are morphologically good but physiologically quite bad. The other segment of the same chromosome, on the contrary, is less dangerous for the growth and allows germination, passage through the style and fertilization, even if it is present in duplicate. — In view of these *Datura* results, it is quite evident that the occurrence of structural differences in a population will largely cause a selective pollen

tube growth. In many cases the pollen will probably also be quite inferior in morphological or at least in physiological respects.

If structural differences are frequent, the pollen quality of cross-fertilizers should, on an average, be less good than in the homozygous, selected biotypes of autogamous species, in which the effect of the structural differences will only appear in the F_1 hybrids between different lines. In order to elucidate this problem comparative pollen investigations of some cross- and self-fertilizing species were commenced in the preceding summer. In the first place some diploid species were chosen for that purpose. In polyploid species, which are always to be regarded as partially autopolyploid (cf. MÜNTZING, 1937 b), it is less probable that the structural changes possibly occurring will result in visible pollen abortion.

In the material studied the self-fertilizers were represented by barley and *Triticum monococcum*, the cross-fertilizers by rye, red clover, white clover and mangels. The result obtained will be considered in detail on another occasion. Already now it may be stated, however, that the difference between the two categories was quite striking and of the kind expected. Thus, 59 barley individuals, representing 12 different varieties, had an average of 95,0 per cent good pollen, and just the same good fertility was found in *Triticum monococcum*. In rye, on the contrary, all mean values were lower, and on an average more than half of the 252 population plants examined were partially sterile, *i. e.* having more than 10 per cent bad pollen. Partial pollen sterility of widely different degrees was also found to be quite frequent in the other cross-fertilizers tested. Various populations in the same species gave somewhat different values, but on an average the contrast between the auto- and allogamous species was entirely beyond dispute. Though the pollen studies must be extended to include a greater number of species it is highly probable, already now, that this difference in average pollen fertility is of general occurrence, at least with respect to species with low chromosome numbers.

In rye, seed-setting after open pollination was also examined. Partial sterility is evidently also met with on the female side, and this female sterility was found to be correlated with the pollen sterility. From this and other results it is perfectly clear that the partial sterility, occurring in rye populations, has specific genotypical causes. It has not yet been proved that these genotypical causes consist of structural chromosome differences, but in analogy with the other facts discussed above this is highly probable.

Thus, in a cross-fertilizer such as rye the pollen evidently comprises different classes of gametes with different viability. Several combinations are quite unviable and appear as empty pollen grains, others are morphologically different. With respect to the latter category pollen tube growth is probably selective, *i. e.* certain pollen types are well suited to certain stigmas but not functional on others.

The investigations on the nature and inheritance of self-sterility, in particular, have demonstrated that pollen tube growth is conditioned by a reciprocal reaction between the male gametophyte and the stylar tissue, the result under such circumstances being dependent on the genotypical constitution of both these components. It seems probable that also in a cross-fertilizer like rye the most favourable reaction between style and pollen tube will be obtained provided their constitutions are complementary to each other. This would imply that if a certain individual is heterozygous for a small deficiency or some other structural disturbance of the balance, pollen grains with the same structural deviation will not function on this plant or at least be inferior in competition with pollen grains of a different constitution. Thus, in the favourable cases pollen tube growth would be stimulated by a *complementary reaction.* This reaction may perhaps be compared to the complementary reaction causing an increased vigour in F_1 of a cross between two different inbred lines. — The occurrence of such a selective pollen tube growth would evidently tend greatly to keep up heterozygosity in a population, those pollen types being favoured which differ in constitution as much as possible from the plant pollinated.

If, on the contrary, a plant is isolated, the rich assortment of male gametes present in the population is not available, but the plant has to manage with the types of male gametes it is capable of forming by recombination. With respect to these gametes two possibilities may occur, *viz.* that it is a question of one or several structural differences. If there is only one such structural deviation, which may be denoted by *a*, the plant in question will have the constitution *Aa.* In the pollen the *a* gametes will be poor, whereas in the ovules *a* as well as *A* are probably functional. On the assumption that there is plenty of pollen and hence sufficient quantities of *A* gametes on the different parts of the stigmas, the progeny after isolation of such an *Aa* individual would approximately consist of 1 *AA* : 1 *Aa.* Thus, if one assumes only one structural difference, open pollination and selfing should give about the same result.

If, however, as is more probable, several small structure differences

are involved (their number = n), most of the gametes will contain some of these alterations and only $1 : 2^n$ of the gametes will be completely devoid of such changes. According to the hypothesis, this would mean that only a fraction of the pollen of a certain plant would have a quite normal pollen tube growth when used for selfing (though it might be partly or entirely successful on plants with a different constitution). Under such circumstances it is probable that also part of the »defective» types of gametes will function, since most of the pollen is of that kind. On account of the unsuitable constitution of the plant's own pollen selfing will, firstly, give a poor seed setting and, secondly, a progeny with a reduced average vigour, part of the daughter plants becoming more or less homozygous with respect to the deleterious structural deviations.

Thus, the new point of view presented by the preceding arguments is the idea that the high viability and maximal heterozygosity of the population plants is largely preserved thanks to selective pollen tube growth. This process will rather effectively prevent the occurrence of homozygosity for the structural deviations. Upon inbreeding such homozygosity will in part arise, because the pollen competition will be diminished and some more or less defective pollen classes have a chance to function. Thus, at least in part *the inbreeding degeneration upon selfing would be caused by homozygosity for the same structure alterations which in the open pollinated populations regulate a selective pollen tube growth.*

It is possible that several other circumstances are responsible for the inbreeding phenomena. At any rate, the points of view here presented, which are founded on the theory of frequent structural differences in populations, must be discussed and tested in connection with future investigations concerning the causes of inbreeding degeneration.

From the view that selective pollen tube growth in a cross-fertilizer is caused by structural differences in the populations it is not a far step to suspect that the same cause, at least in part, may be responsible for the *self-sterility phenomena.* According to the very thorough investigations performed by EAST and other workers, self-sterility in *Nicotiana* and some other genera is controlled by systems of multiple allels, the allels present in the pollen grains deciding whether the pollen grain will be capable of functioning in a certain style. Thus, as is well known, a plant with the constitution $s_1\, s_2$ cannot successfully be fertilized by s_1 or s_2 pollen but only by pollen grains carrying other allels (s_3, s_4, etc.).

Now, if these recessive allels represent structural deviations, it may

be imaginated that, as in the cross-fertilizers suffering from inbreeding, a favourable reaction will only by obtained if the genes in style and pollen grain complete each other, two identical defects, on the contrary, leading to an unfavourable reaction and a checked pollen tube growth. This inhibiting reaction would, indeed, be very expedient and, just as in rye and other cross-fertilizers, prevent homozygosity for structural defects. A very strong indication that this suggestion contains at least a grain of truth is the fact that self-sterility allels in a homozygous condition as a rule, though not always, have a more or less lethal effect. This is true, of *Nicotiana* (EAST and MANGELSDORF, 1926; EAST, 1927) as well as *Petunia* (HARLAND and ATTECK, 1933; cf. also SEARS, 1937) and *Prunus* (CRANE and BROWN, 1937). This lethal effect is, indeed, a most interesting feature, which certainly must be of great importance for an understanding of the real nature of the self-sterility factors. It is in excellent accordance with the theory advanced in the present paper that intraspecific differences in chromosome structure are frequent, these differences being responsible for sterility, meiotic irregularities, inbreeding degeneration and selective pollen tube growth.

VII. SUMMARY.

1) Following up previous investigations of intraspecific sterility in *Galeopsis*, pollen fertility in 66 different F_1 combinations was examined. These combinations were obtained by crossing 12 pure lines of *Galeopsis Tetrahit* in all possible directions.

2) In contrast to the parent lines the F_1 combinations are often partially sterile. Thirty of the 66 combinations had 90—100 per cent good pollen, the other crosses giving partially sterile hybrids with a pollen percentage ranging from 50 to 89.

3) Each F_1 combination is characterized by a certain degree of fertility. Previous investigations seemed to indicate that the F_1 combinations were either fertile, semi-sterile or quarter-sterile. From the present results it is evident that there are no limits between these categories. Thus, with respect to the degree of fertility there are continuous transitions between marked sterility and slight decreases in fertility, which are difficult to demonstrate.

4) The causes leading to sterility of the F_1 hybrids are distributed all over the lines and not only characteristic of a few of them. However, there are significant line differences as to degree and frequency of sterility in combination with the other lines.

5) With respect to the causes of sterility the 12 lines represent at least 9 or 10 different types. If only the relative similarity is considered, the lines may be arranged into two groups comprising 4 and 5 lines, the remaining 3 lines being quite independent. This approximate group division is not correlated with morphological similarities. The geographical origin is also of little or no importance.

6) A significant positive correlation was found between the degree of fertility in the F_1 generations and the degree of similarity with which the parent lines react with other lines. Thus, the percentage of good pollen in a certain F_1 combination is a good expression of the degree of constitutional similarity between the parent lines with respect to the causes of sterility.

7) A case of genotypically controlled sterility of the same kind as in *G. Tetrahit* was also observed in *G. speciosa.*

8) Cytological investigations demonstrate that the 32 chromosomes of the *Tetrahit* lines almost always form 16 bivalents at meiosis. However, in about 8 per cent of the metaphase groups there were one or generally two univalents.

9) In nine F_1 generations, cytologically studied, the frequency of univalents was higher than in any of the pure lines, the total average value being 49 per cent. Different F_1 combinations gave widely different frequencies.

10) In some F_1 hybrids a varying number of complete metaphase groups could be analysed. Multivalents, especially trivalents, and configurations deviating from the normal condition with 16_{II} were often met with. Some F_1 generations were characterized by the prevalence of certain deviating configurations such as $1_{III} + 14_{II} + 1_{I}$.

11) In a certain F_1 combination with a high frequency of unpaired chromosomes these univalents were found to differ considerably in size in contrast to the conditions in the pure lines.

12) There is no clear correlation between univalent frequency and pollen sterility. The occurrence of univalents at meiosis and ensuing irregularities is not the essential cause of sterility. Disturbed chromosome pairing and reduced fertility are, rather, different symptoms of the same cause, *viz.* structural differences between the lines crossed.

13) Cytological investigations in the diploid species *G. speciosa* showed a normal meiosis in some fertile individuals. Especially in one of the partially sterile plants the frequency of univalents was increased, and in the same plant there were associations of four chromosomes in about half of the metaphase groups. Thus, as in *G. Tetrahit* sterility

and meiotic irregularities are in this case caused by heterozygosity for structural differences.

14) The immediate cause why pure lines of *G. Tetrahit* are very often structurally dissimilar is probably hybridization with the related species *G. bifida.*

15) The results in *Galeopsis* and other genera demonstrate that in addition to the very marked and therefore first observed cases of intraspecific sterility, due to structural differences, there is another category, in which sterility as well as the cytological complications are less apparent. In the latter cases, which are much more frequent than generally assumed, the structural differences are quantitatively more or less insignificant.

16) The frequent occurrence of structural differences in auto- as well as allogamous species is important for certain general problems of genetics, such as the inbreeding phenomena. Thus, there is reason to assume, for instance, that the inbreeding degeneration upon selfing is caused by homozygosity for the same structural alterations which in the open pollinated populations regulate a selective pollen tube growth.

Svalöf, Institute of Genetics, November 1937.

LITERATURE CITED.

1. ANDERSON, E. and SAX, K. 1936. A cytological monograph of the American species of *Tradescantia.* — Bot. Gazette, Vol. 97, No. 3, pp. 433—476.
2. BABCOCK, E. B. and EMSWELLER, S. L. 1936. Meiosis in certain interspecific hybrids in *Crepis* and its bearing on taxonomic relationship. — Univ. Calif. Publ. Agricult. Sciences, Vol. 6, No. 12, pp. 325—368.
3. BAUER, H. 1936. Beiträge zur vergleichenden Morphologie der Speicheldrüsenchromosomen. — Zoologische Jahrbücher, Bd. 56, H. 3, pp. 239—276.
4. — 1937. Cytogenetik. — Fortschritte der Zoologie, Bd. II. — (In the press.)
5. BERGNER, A. D. and BLAKESLEE, A. F. 1932. Cytology of the *ferox—quercifolia—stramonium* triangle in *Datura.* — Proc. Nat. Acad. Sciences, Vol. 18, No. 2, pp. 151—159.
6. BERGNER, A. D., SATINA, S. and BLAKESLEE, A. F. 1933. Prime types in *Datura.* — Proc. Nat. Acad. Sciences, Vol. 19, No. 1, pp. 103—115.
7. BLAKESLEE, A. F. 1928. Genetics of *Datura.* — Verhandl. V. intern. Kongr. für Vererb.-wissenschaft, Berlin 1927. Bd. I.
8. — 1934. New Jimson weeds from old chromosomes. — Journ. of Heredity, Vol. 25, No. 3, pp. 80—108.
9. BRINK, R. A. and COOPER, D. C. 1932. A structural change in the chromosomes of maize leading to chain formation. — Am. Nat., Vol. LXVI, pp. 310—322.

10. BUCHHOLZ, J. T. and BLAKESLEE, A. F. 1930. Pollen-tube growth of the primary mutant of *Datura*, Rolled, and its two secondaries. — Proc. Nat. Acad. Sciences, Vol. 16, No. 3, pp. 190—195.
11. BURNHAM, C. R. 1932. An interchange in maize giving low sterility and chain configurations. — Proc. Nat. Acad. Sciences, Vol. 18, No. 6, pp. 434—440.
12. CLARKE, A. E. and ANDERSON, E. G. 1935. A chromosomal interchange in maize without ring formation. — Am. Journ. of Botany, Vol. 22, p. 711—716.
13. CLAUSEN, J. 1926. Genetical and cytological investigations in *Viola tricolor* L. and *V. arvensis* MURR. — Hereditas VIII, pp. 1—156.
14. — 1931. Cyto-genetic and taxonomic investigations on *Melanium* violets. — Hereditas XV, pp. 219—308.
15. CRANE, M. B. and BROWN, A. G. 1937. Incompatibility and sterility in the sweet cherry, *Prunus avium*, L. — Journ. of Pomology and Horticult. Science, Vol. 15, No. 2, pp. 86—116.
16. DARLINGTON, C. D. 1931. The analysis of chromosome pairing in *Triticum* hybrids. — Cytologia, Vol. 3, No. 1, pp. 21—25.
17. — 1933. The origin and behaviour of chiasmata, VIII. *Secale cereale* ($n = 8$). — Cytologia, Vol. 4, No. 4, pp. 444—452.
18. — 1936. Crossing over and its mechanical relationships in *Corthippus* and *Stauroderus*. — Journ. of Genetics, Vol. 33, H. 3. pp. 465—500.
19. — 1937. Recent advances in cytology. Second edition. — Churchill, London.
20. DEMEREC, M. 1937. Relationship between various chromosomal changes in *Drosophila melanogaster*. — Cytologia, FUJII Jubilee Volume, pp. 1125—1132.
21. DUBININ, N. P., HEPTNER, M. A., DEMIDOVA, Z. A. and DJACHKOVA, L. S. 1936. Genetic constitution and gen-dynamics of wild populations of *Drosophila melanogaster*. — Biologicheskij Zhurnal, Bd. 5, No. 6, pp. 939—976.
22. DUBININ, N. P., SOKOLOV, N. N. and TINIAKOV, G. G. 1936. Occurrence and distribution of chromosome aberration in nature (*Diptera*). — Nature, June 1936, pp. 1035—1036.
23. EAST, E. M. 1927. Peculiar genetic results due to active gametophyte factors. — Hereditas IX, pp. 49—58.
24. EAST, E. M. and MANGELSDORF, A. J. 1926. Studies on self-sterility. VII. Heredity and selective pollen-tube growth. — Genetics, Vol. 11, pp. 466—481.
25. ERLANSON, E. W. 1933. Chromosome pairing, structural hybridity, and fragments in *Rosa*. — Bot. Gazette, Vol. 94, No. 3, pp. 551—566.
26. GAIRDNER, A. E. and DARLINGTON, C. D. 1930. Structural variation in the chromosomes of *Campanula persicifolia*. — Nature, January 1930, pp. 1—4.
27. GEITLER, L. 1937. Cytogenetische Untersuchungen an natürlichen Populationen von *Paris quadrifolia*. — Zschr. f. ind. Abst.- u. Vererb.-lehre, Bd. 73, H. 2, pp. 182—197.
28. HARLAND, S. C. and ATTECK, O. S. 1933. The inheritance of selfsterility in *Petunia violacea*. — Genetica, Bd. 15, pp. 89—102.
29. HOLLINGSHEAD, L. 1932. The occurrence of unpaired chromosomes in hybrids between varieties of *Triticum vulgare*. — Cytologia, Vol. 3, No. 2, pp. 119—141.
30. HOSONO, S. 1935. Karyogenetische Studien bei reinen Arten und Bastarden der Emmerreihe. — Jap. Journ. of Bot., Vol. VII, No. 3—4, pp. 301—322.

31. HÅKANSSON, A. 1931. Über Chromosomenverkettung in *Pisum*. — Hereditas XV, pp. 17—61.
32. KOLLER, P. C. 1937. The genetical and mechanical properties of sex chromosomes. III. — Man. — Proc. of the Royal Society of Edinburgh, Vol. 57, No. 14, pp. 194—214.
33. LEVAN, A. 1936. Die Zytologie von *Allium cepa* × *fistulosum*. — Hereditas XXI, pp. 195—214.
34. MÜNTZING, A. 1929. Cases of partial sterility in crosses within a Linnean species. — Hereditas XII, pp. 297—319.
35. — 1930 a. Outlines to a genetic monograph of the genus *Galeopsis*. — Hereditas XIII, pp. 185—341.
36. — 1930 b. Über Chromosomenvermehrung in *Galeopsis*-Kreuzungen und ihre phylogenetische Bedeutung. — Hereditas XIV, pp. 153—172.
37. — 1932 a. Disturbed segregation ratios in *Galeopsis* caused by intraspecific sterility. — Hereditas XVI, pp. 73—104.
38. — 1932 b. Cyto-genetic investigations on synthetic *Galeopsis Tetrahit*. — Hereditas XVI, pp. 105—154.
39. — 1934. Chromosome fragmentation in a *Crepis* hybrid. — Hereditas XIX, pp. 284—302.
40. — 1936. The evolutionary significance of autopolyploidy. — Hereditas XXI, pp. 263—378.
41. — 1937 a. Multiple allels and polymeric factors in *Galeopsis*. — Hereditas XXIII, pp. 371—400.
42. — 1937 b. The effects of chromosomal variation in *Dactylis*. — Hereditas XXIII, pp. 113—235.
43. NAVASHIN, M. 1934. Chromosome alterations caused by hybridization and their bearing upon certain general genetic problems. — Cytologia, Vol. 5, No. 2, pp. 169—203.
44. NILSSON, HERIBERT. 1937. Eine Prüfung der Wege und Theorien der Inzucht. — Hereditas XXIII, pp. 236—256.
45. RANCKEN, G. 1934. Zytologische Untersuchungen an einigen wirtschaftlich wertvollen Wiesengräsern. — Acta Agralia Fennica 29, pp. 1—92.
46. RHOADES, M. M. and MCCLINTOCK, B. 1935. The cytogenetics of maize. — Botan. Review, Vol. 1, pp. 292—325.
47. SANSOME, F. W. and PHILP, J. 1932. Recent advances in plant genetics. — Churchill, London.
48. SEARS, E. R. 1937. Cytological phenomena connected with self-sterility in the flowering plants. — Genetics, Vol. 22, No. 1, pp. 130—181.
49. STADLER, L. J. 1932. On the genetic nature of induced mutations in plants. — Proc. of the sixth intern. congr. of Genetics, Vol. 1, pp. 274—294.
50. — 1933. On the genetic nature of induced mutations in plants. II. A haploid-viable deficiency in maize. — Univ. of Missouri, Coll. of Agricult., Research Bull. 204, pp. 1—29.
51. SWESHNIKOWA, I. N. 1929. *Vicia sativa* L. and *Vicia cracca* L. — Annals of Timiriasev Agricult. Acad., Vol. 4, pp. 1—21.
52. — 1932. A study of interspecific hybrids of *Vicia*. — Proc. 6th Int. Congr. Gen. Ithaca.

53. THOMPSON, W. P. and ROBERTSON, H. T. 1930. Cytological irregularities in hybrids between species of wheat with the same chromosome number. — Cytologia, Vol. 1, No. 3, pp. 252—262.

54. VAKAR, B. A. 1932. Cytological study of the interspecific hybrids of the genus *Triticum*. — Bull. of appl. Botany, of Genetics and Plant-breeding, Series 2, No. 1, pp. 189—241.

CONTENTS.

I. Introduction 117

II. Pollen fertility in pure lines and F_1 combinations in *Galeopsis Tetrahit* .. 118

1. Pure lines 118

2. F_1 combinations 119

A. Frequency and degree of partial sterility 119

B. Group delimitation 124

C. Correlation between group delimitation, morphology and geographical origin 127

D. Correlation between reaction ratio and pollen fertility 129

III. A case of intraspecific sterility in *Galeopsis speciosa* 131

IV. Cytological investigations in *Galeopsis Tetrahit* 135

1. Chromosome pairing in pure lines 135

2. Chromosome pairing in the F_1 combinations 138

A. Frequency of univalents 138

B. Configurations in different F_1 hybrids 140

C. The relative size of the univalents in the hybrids between the *B* and *G* lines 144

D. Correlation between pollen sterility and meiotic irregularities 150

V. Cytological investigations in *Galeopsis speciosa* 151

VI. Discussion 156

1. Evidence that intraspecific sterility in *Galeopsis* is due to differences in chromosome structure 156

A. Introduction 156

B. Definite configurations in the F_1 hybrids 157

C. The frequency of univalents 159

D. Univalents of different size 160

E. Is sterility a consequence of interspecific pairing? 161

2. Why are structural differences frequent in *G. Tetrahit*? 163

3. The degree and frequency of intraspecific sterility in *Galeopsis* 165

4. Cytological disturbances and intraspecific sterility in some other genera 168

A. Different degrees of structural alterations and their effects 168

B. STADLER's investigations of induced mutations 171

C. Increased univalent frequency as evidence of structural differences 173

D. A theory concerning the connection between the occurrence of frequent structural differences and the inbreeding phenomena 177

VII. Summary 183

Literature cited 185

A NEW GIANT POPULUS TREMULA IN NORRBOTTEN

BY *YNGVE MELANDER*
LUND, SWEDEN

THE locality of these giant aspens is situated in the Province of Norrbotten about 15 kilometres north-west of Boden. The land belongs to the Agricultural School of Vittjärvsgården owned by the Luossavaara Kiirunavaara Ltd.

The aspens were discovered in a season quite unusual for making botanical discoveries. Last Christmas (1936) when ski-ing in that part of the country I happened to come to the spot where the trees grew, which at once attracted my attention. To begin with the aspens were unusually tall, and besides they had a remarkably massive growth and structure. On closer examination the buds turned out to be of a size not usual for this tree. It was especially this latter circumstance which at once made me surmise that I had discovered a new type of triploid aspen ($2n = 57$).

I sent some twigs from one of the trees to Svalöf, where Professor NILSSON-EHLE had the chromosome number counted. This was carried out by Mr. GÖSTA TOMETORP by means of cells from leaf-stalks (TOMETORP, 1937). This unsuitable method had to be resorted to, as neither root-tips nor catkins could be obtained.

The clone has an extraordinarily wide distribution and is certainly old. It includes about 60 tall trees besides young trees and lots of root-cuttings. The trees grow within an area of about 300 metres extending along the slope of a low mountain bordering on a fen just below. The soil is composed of block moraine and is very meagre, judging from the growth of the fir-trees in the same locality. The altitude is about 175 metres above the sea-level.

The tallest trees are more than 20 metres in height, and are at breast-height 50 to 60 centimetres in diameter. A cut aspen — not one of the tall ones — 117 years old, was at breast-height 40 centimetres in diameter and 19,7 metres from root to top. It yielded a log which was 16,55 metres long and 4 inch. at the top end, quite straight, and with absolutely sound timber.

The growth is particularly beautiful from an architectonic point of

view (Fig. 1), one straight, tapering main-stem with perpendicular, short side-branches. The bark of the upper three-fourths of the tree is smooth and light yellowish green in colour. The bark of very young trees is yellowish green all over.

Sometimes the remarkably big buds (Fig. 2) have up to 12 bud-scales. They contain also a very large number of leaves, viz. 5—11 each. The leaves are of pronounced *villosa*-type, just burst out they are white-lanate.

Fig. 1. Giant aspens at Vittjärv. April, 1937.

The form of the leaves of the giant aspens resembles that of the normal aspens growing in the immediate neighbourhood (Fig. 3). Measurements of about 50 leaves from both sorts of tree showed that the length and breadth of the leaf-disk of the giant aspen were on an average 88 mm. and 89 mm. respectively and of the diploid aspen 60 mm. and 61 mm. The surface of the leaves of the giant aspen has somewhat more than twice the area of that of the normal aspen. The leaf-stalks are comparatively shorter, with an average length of 64 mm., while those of the diploid sort are 51 mm. Moreover, the leaves are strikingly thick and are dark green in colour.

The length of the stomata of the giant aspen and the normal aspen

from the same locality was measured in water upon the epidermis from dry autumn leaves, which had been boiled in lactic acid. As was to be expected, the giant aspen had larger stomata than the normal kind (Table 1). The proportion was 127 to 100. In the giant aspen the length was 8,08 units and in the diploid aspen 6,36 units.

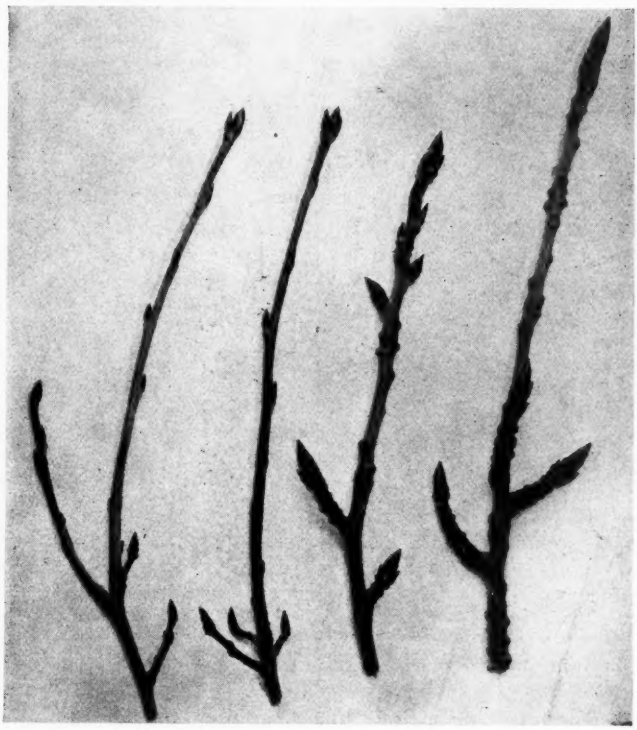


Fig. 2. Two twigs of normal aspen (left) and of giant aspen (right). April, 1937.

TABLE 1. *Length of stomata in diploid and triploid Populus tremula.*

	Length of stomata (units)											n	M ± m	Relative values
	3	4	5	6	7	8	9	10	11	12	13			
Vittjärv normal	2	3	7	12	19	4	2	1				50	6,36 ± 0,13	100
Vittjärv *gigas*		1	1	4	11	16	10	4	1	1	1	50	8,08 ± 0,18	127

1 unit = 2,5 μ.

In order to compare the rate of growth, two free-growing aspens were cut quite near one another, one triploid and one diploid. The average distance between the annual rings of the former was 2,0 mm., and that of the latter 1,4 mm. A cutting of a giant aspen, four years old, was found to have a length of 383 cm. from root to top. The low absolute rate of growth of the giant aspens at Vittjärv must be due to the unfavourable situation and the meagre soil of their present locality.

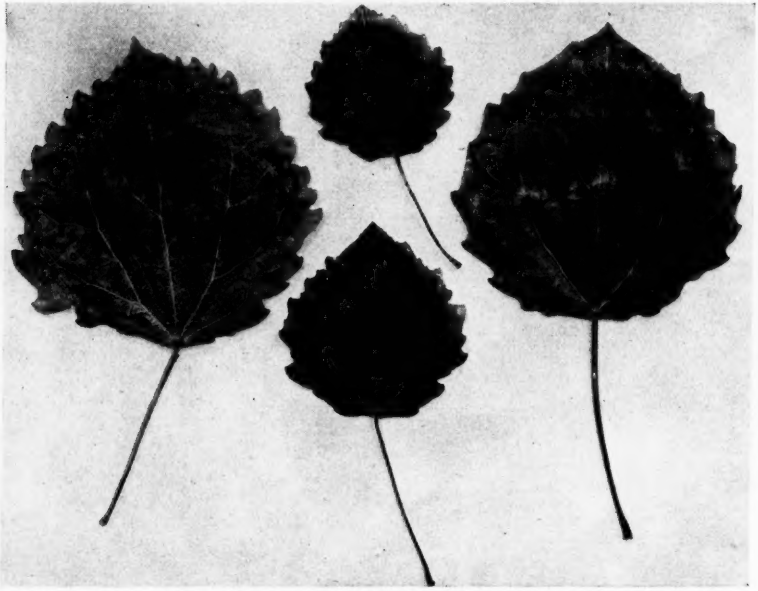


Fig. 3. Leaves of triploid aspen (right and left) and of diploid aspen (centre) from the same locality.

Thus normal aspens in the lowlands a few kilometres to the south have a rate of growth which is greater than that of the giant aspens, where they now are growing.

As mentioned above, flower-buds could not be procured in the winter of 1936—37 in spite of the most careful search. Nor could any flowers be observed during the spring. Therefore it is rather probable that no flowering took place in the spring of 1937. Quite recently (November, 1937) Dr. NILS SYLVÉN has visited the giant aspens at Vittjärv. This winter flower-buds could be obtained, and it was found that the giant aspens are male. The two types of giant aspen

previously known, one in the Province of Skåne (NILSSON-EHLE, 1936 and MÜNTZING, 1936 b) and one in the Province of Medelpad (BLOMQVIST, 1937), are both male, too.

In the spring of 1937 some cuttings of the giant aspen were grafted onto *Populus tremula* v. *erecta* at Svalöf. There it was found that the leaves are very susceptible to rust-disease. In the Norrland locality this susceptibility is of little importance, as these trees, like normal aspens, are but very slightly affected by rust.

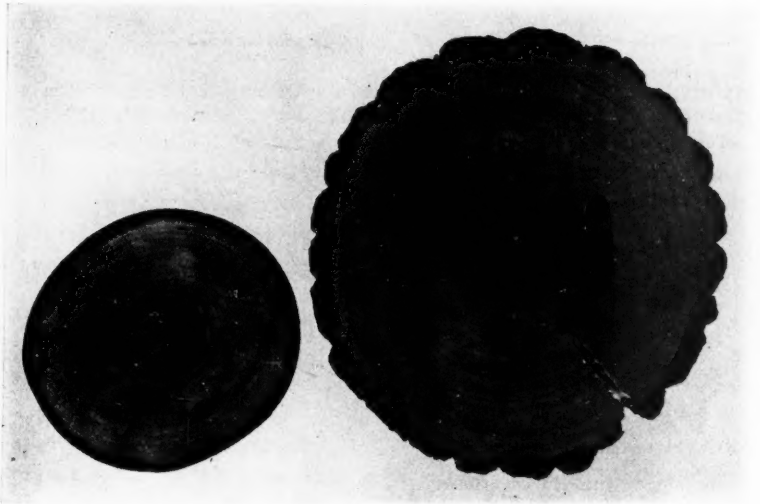


Fig. 4. Sections of giant aspen (right) and of normal aspen (left) from the same locality. The diploid infected by *Polyporus*.

On the other hand, the giant aspens are evidently very resistant to *Polyporus*. In cut trees and on boring it appeared that while the wood of all the triploid aspens examined was sound all through, all the diploid aspens were, as a rule, severely infected by *Polyporus* (Fig. 4).

It is evident that this kind of aspen by being triploid has got better qualities than the neighbouring diploid aspen, out of which it has probably arisen. The single, straight main-stem and the sound wood are qualities which protect the branches from being broken off by snow and winds, which happens exceedingly often to the diploid sort of aspen in the neighbourhood. In spring the numerous leaves of the buds at once provide the trees with a dense foliage, which of course enables

them to profit by the short summer. Finally, the disinclination of the aspens to flower saves much material which is useful to the vegetative parts of the trees.

LITERATURE CITED.

1. BLOMQVIST, S. G:SON. 1937. Ett fynd av jätteasp (*Populus tremula gigas*) i Medelpad. — Botaniska Notiser 1937, pp. 119—123.
2. MÜNTZING, A. 1936 a. The evolutionary significance of autopolyploidy. — Hereditas XXI, pp. 263—378.
3. — 1936 b. The chromosomes of a giant *Populus tremula*. — Hereditas XXI, pp. 383—393.
4. NILSSON-EHLE, H. 1936. Über eine in der Natur gefundene Gigasform von *Populus tremula*. — Hereditas XXI, pp. 379—382.
5. TOMETORP, G. 1937. The chromosome numbers of two new giant *Populus tremula*. — Botaniska Notiser 1937, pp. 285—290.

DARSTELLUNG TETRAPLOIDER ÄPFEL UND IHRE BEDEUTUNG FÜR DIE PRAKTISCHE APFELZÜCHTUNG SCHWEDENS

VON *H. NILSSON-EHLE*
INSTITUT FÜR VERERBUNGSFORSCHUNG, SVALÖF

FÜR die Obstbaumzüchtung Schwedens ist die Darstellung *lange haltbarer* und gleichzeitig in anderen praktischen Hinsichten wertvoller und dem schwedischen Klima gut angepasster neuer Apfelspätsorten von besonderem Interesse. Nachdem HEILBORN (1935) gezeigt hat, dass die triploiden Apfelsorten durchschnittlich eine deutlich längere Haltbarkeit als die diploiden Sorten besitzen, muss daher die Darstellung *neuer* triploider Sorten in grosser Anzahl als Grundlage einer umfassenden und effektiven Auslese in oben erwähnter Richtung ein Hauptmoment dieser Züchtungslinie sein.

Für die absichtliche Darstellung neuer triploider Sorten sind verschiedene Wege denkbar. Der unten beschriebene Weg ist die absichtliche Darstellung *tetraploider* Sorten in möglichst grosser Zahl, die dann u. a. dazu verwendet werden sollen, durch Kreuzung mit besonders angezeigten, wertvollen diploiden Sorten das umfassende neue triploide Auslesematerial hervorzuschaffen. Auf diese Weise wird es möglich sein, ein besonders grosses solches triploides Auslesematerial zu erhalten, das allmählich die im Obstbau erwünschten Spätsorten liefern könnte.

Die absichtliche Darstellung tetraploider Sorten ist nun auch in verschiedener Weise auszuführen. Am einfachsten scheint die Herstellung vereinzelter tetraploider Individuen aus triploiden Sorten durch Aufziehung grosser Nachkommenschaften derselben. Diese Methode ist nach den grundlegenden Untersuchungen ROSENBERGS (1927) über die semiheterotypische Teilung und Restitutionskerne besonders naheliegend, weil man annehmen kann, dass bei triploiden Sorten vereinzelte unreduzierte, d. h. triploide Gameten nicht gar zu selten gebildet werden, die dann durch Befruchtung mit Pollen gewöhnlicher diploider Sorten Tetraploiden ergeben. Auch durch Verbindung triploid × triploid ist allerdings Bildung von Tetraploiden aus Befruchtung zweier diploiden Gameten möglich; in der Tat hat ja NEBEL (1933) durch Kreuzung

triploid × triploid schon bei einer nicht sehr grossen Nachkommenzahl annähernde Tetraploiden (höchste Anzahl 64 Chromosomen) bekommen.

Auf welchem von diesen beiden Wegen die Tetraploiden mit 68 Chromosomen hergestellt werden, hat vielleicht nicht so grosse praktische Bedeutung, wenn nur Tetraploiden in nicht zu geringer Zahl geschaffen werden können.

In Anbetracht der von CRANE und LAWRENCE (1934) zusammengestellten Data über das allgemeine Verhalten triploider Apfelsorten mit Hinsicht auf Fertilität, Samenkeimung u. s. w., schien es mir angezeigt, beim Institut für Vererbungsforschung, Svalöf, eine Spezialuntersuchung besonders wertvoller in den besten Obstbaugebieten Südschwedens in grossem Umfang angebauter triploider späterer Qualitätssorten ausführen zu lassen. Zu diesem Zweck wurden in erster Linie die beiden späten Qualitätssorten *Belle de Boskoop* und *Blenheim* zum Objekt der Untersuchung gewählt. Durch gütige Vermittlung der Herren Bureaudirektor SONESSON, Stockholm und Gartenbaukonsulent PERSSON, Kristianstad, erhielt das Institut von der Sorte *Boskoop*, Ernte 1936, eine zusammmengebrachte Menge von 2.200 Kg., von *Blenheim* 1.000 Kg., die insgesamt rund 80.000 Samen ergaben. Für diese Vermittlung sei hier im Namen des Institutes der beste Dank ausgesprochen. Die genauen Zahlen der ausgesäten Samen und den daraus entwickelten Pflanzen sind die folgenden:

	März—April 1937 ausgesäte Samen		Entwickelte Pflanzen	
Boskoop volle Samen	34.650		2.455	
» runzlige Samen	30.931	65.581	46	2.501
Blenheim volle Samen	11.205		1.514	
» runzlige Samen	3.001	14.206	38	1.552
Summe		79.787		4.053

Die Untersuchung wurde infolge des damit verbundenen praktischen Zieles Gegenstand lebhaften Interesses von Seiten der schwedischen Presse (siehe zum Beispiel Svenska Dagbladet 23. Jan. und 15. März 1937, Skånska Dagbladet 5. Febr. 1937, Sydsvenska Dagbladet 15. März 1937, u. s. w.), wo u. a. die vom Verf. gehegte Hoffnung, tetraploide Pflanzen zu erhalten, besonders hervorgehoben wurde. In meinem Vortrag im schwedischen pomologischen Verein am 14. März 1937 wurden auch die beim Institut für Vererbungsforschung laufenden Versuche, um tetraploide Äpfel zu erhalten, sowie auch das oben erwähnte Ziel dieser Untersuchungen näher erörtert.

Es ist deshalb erfreulich, dass diese Erwartungen, Tetraploiden zu erhalten, jetzt vollauf erfüllt wurden, indem in dem bis jetzt untersuchten Material, wie schon in der Presse mitgeteilt wurde (Nya Dagl.

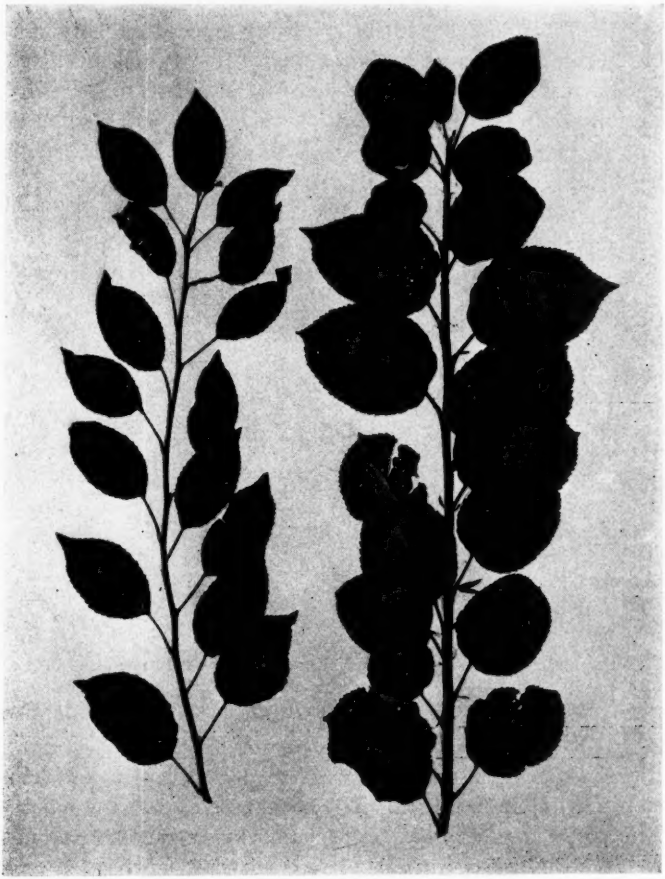


Fig. 1. Zweige erwachsener Bäume von *Cox Orange* (diploid) links und *Blenheim* (triploid) rechts, im Garten des Svalöfer-Instituts angebaut.

Allehanda 19. November 1937), schon mehrere Tetraploiden gefunden worden sind.

Die Untersuchung der Chromosomenzahl wurde Fil. Kand. INGRID BERGSTRÖM anvertraut, die in einer hier anschliessenden Abhandlung (1938) darüber Näheres berichtet.

Da nach früheren Untersuchungen über die Nachkommenschaft triploider Apfelsorten (vgl. CRANE und LAWRENCE, 1934) die Mehrzahl der Nachkommen von Triploiden aneuploid sind und in der Regel eine schwächere Entwicklung zeigen als diploide und triploide Pflanzen, wurden die Tetraploiden natürlich speziell unter den besonders kräftigen Pflanzen nachgesucht. Vor allem wurden Pflanzen mit verhältnismässig grossen, breiten, gerundeten Blättern untersucht, weil schon die bekannten triploiden Apfelsorten durchschnittlich in dieser Richtung von den diploiden Sorten deutlich abweichen (vgl. Fig. 1). Selbstverständlich ist dieser Unterschied zwischen den diploiden und triploiden Gruppen nur durchschnittlich. Wie gewöhnlich greifen nämlich offenbar die diploide und die triploide Variationskurve stark in einander hinein, weil die Blattgrösse sowie andere erbliche Eigenschaften nicht nur von der Chromosomenzahl sondern in hohem Maasse auch von der Genkombination beeinflusst wird. Durch Auslese besonders gross- und rundblättriger Pflanzen hat man jedoch grössere Aussichten, triploide und tetraploide Pflanzen in der Nachkommenschaft zu kriegen.

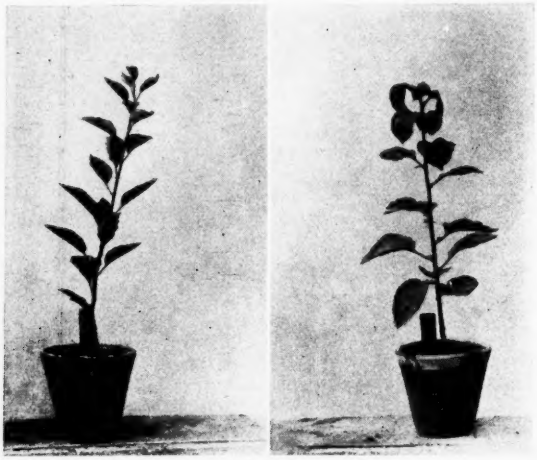


Fig. 2. Tetraploide Pflanze in der Nachkommenschaft von *Boskoop*. Links diploide Pflanze, Bo_1—46 ($2n = 34$); rechts eine von den vier tetraploiden Pflanzen, Bo_1—54 ($2n = 68$). Aufnahme August 1937. Höhe der tetraploiden Pflanze 33 cm. Die grossen Nebenblätter der tetraploiden Pflanze sind deutlich zu sehen.

Wie aus der Darstellung BERGSTRÖMS (1938; Table 2) näher hervorgeht, wurden von der Sorte *Boskoop* bisher 40 solche kräftige Pflanzen untersucht, von denen 27 sicher oder sehr wahrscheinlich die genaue

diploide Zahl 34 erwiesen; 5 Pflanzen waren aneuploid (Zahl 35—41), 2 triploid (51—52), 2 etwas mehr als triploid (55—57) und 4 *sicher tetraploid* (68).

Von der Sorte *Blenheim* wurden vorläufig nur 11 solche kräftige Pflanzen untersucht. Diese waren diploid bis triploid.

Die tetraploiden *Boskoop*-Pflanzen (vgl. Fig. 2—4) unterscheiden sich sämtlich von den genannten diploiden Schwesterpflanzen durch mehr gerundete und flache, vom Stamm mehr rechtwinklig ausstehende, tiefer gezähnte Blätter (vgl. Fig. 3), mit grösseren, breiteren Zähnen. Die oberen Blätter der Tetraploiden sind manchmal zurückgebogen und nach unten etwas eingerollt (vgl. Fig. 2). Bei zwei von den vier Tetraploiden sind die Blätter auch grösser als bei den Diploiden (vgl. Fig. 2). Auch die zwei Tetraploiden, die nicht besonders grossblättrig sind, zeichnen sich durch die gröbere Zähnung der Blätter sowie durch charakteristische breite, grosse Nebenblätter (vgl. unten) aus. Dicke und Farbe der Blätter scheinen sich nicht anders zu verhalten als bei den Diploiden. Dagegen sind die Nebenblätter bei den Tetraploiden der Sorte *Boskoop* (Fig. 4) sehr charakteristisch, vor allem grösser und breiter, aber auch stärker und tiefer gezähnt sowie auch im Herbst später abfallend als bei den diploiden Schwesterpflanzen derselben Nachkommenschaft. Auch triploide Pflanzen (von sowohl *Boskoop* als *Blenheim*) haben bei den Nebenblättern einen ähnlichen, abweichenden Charakter, wenn auch weniger ausgeprägt. Die vier tetraploiden Pflan-

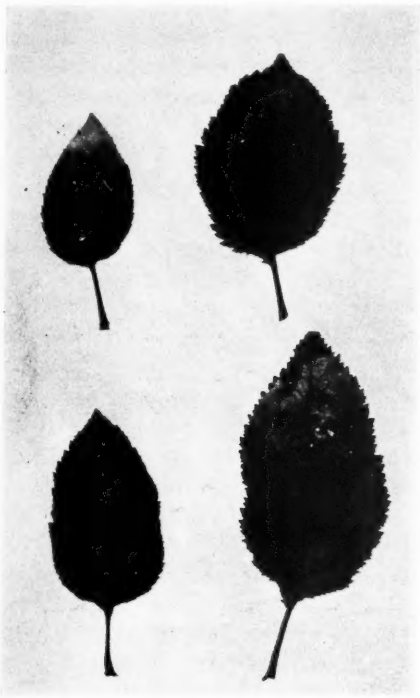


Fig. 3. Zähnung der Blätter bei diploiden (zwei Blätter links) und tetraploiden (zwei Blätter rechts) Pflanzen aus der Nachkommenschaft von *Boskoop*. Links: Pflanze Bo_1—46; rechts, oben: Bo_1—48, unten: Bo_1—54.

zen sind im ersten Jahre nicht höher als die diploiden, eher umgekehrt (vgl. BERGSTRÖM, 1938, Fig. 4). Auch sonst ist am Stamm, wenigstens im ersten Jahre, nichts besonders Auffälliges zu sehen.

Nach dem allgemeinen Aussehen (besonders bei den Nebenblättern) einer Anzahl noch nicht untersuchter Pflanzen sind wahrscheinlich noch mehr Tetraploiden im Material zu erwarten. Von *Boskoop* wurden im Herbst 1937, nachdem die gefundenen Tetraploiden sämtlich die erwähnten grossen Nebenblätter gezeigt hatten, unter den 2.501 Pflanzen noch 73 grössere und kleinere Pflanzen mit verhältnismässig grossen Nebenblättern ausgelesen, die im Frühling 1938, sobald neue Wur-

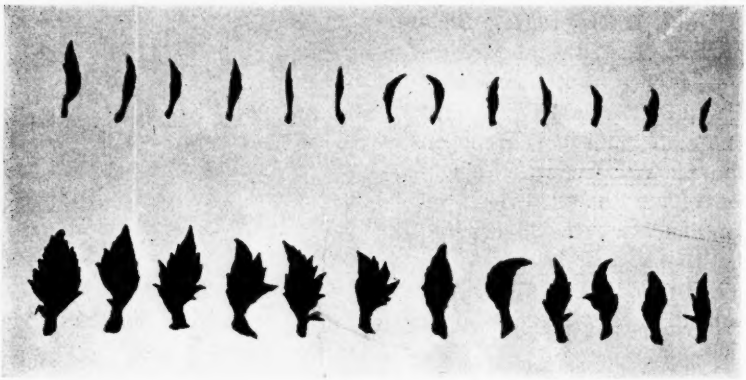


Fig. 4. Nebenblätter einer diploiden (oben) und einer tetraploiden (unten) Pflanze aus der Nachkommenschaft von *Boskoop*. Oben: Pflanze Bo_1—46; unten: Bo_1—54.

zeln gebildet werden, zur Untersuchung kommen werden. Wahrscheinlich finden sich unter diesen Pflanzen sowohl Tetraploiden und Triploiden als auch Aneuploiden. Von *Blenheim* wurden in gleicher Weise 33 Pflanzen mit verhältnismässig grossen Nebenblättern ausgelesen.

Die Nachkommenschaften in ihrer Ganzheit verhalten sich mit Hinsicht auf Variation der Grösse, Kräftigkeit der Pflanzen u. s. w. wie triploide Apfelnachkommenschaften im allgemeinen (nach CRANE und LAWRENCE, 1934). Manche, wahrscheinlich stets aneuploide Pflanzen sind im Typus der Blätter u. s. w. von gewöhnlichen Apfelpflanzen mehr oder weniger stark abweichend. Als Beispiel solcher eigentümlich aussehender Pflanzen können Fig. 5 und 6 dienen. Von Leuten, die diese Versuche ansahen, wurden solche auffällige Varianten, besonders diejenigen in der Nachkommenschaft von *Blenheim* (Fig. 6)

als *Fuchsia-*, *Evonymus-*, *Laurus-*, *Mentha-*, *Acer*-Typen u. s. w. bezeichnet, weil sie mit diesen Pflanzen eine gewisse Ähnlichkeit besitzen. Vom Apfeltypus weichen sie jedenfalls sehr auffällig ab.

Über die Entstehungsweise der vier Tetraploiden kann, da sie aus unkontrollierter Befruchtung hervorgegangen sind, nichts Genaues gesagt werden. Wahrscheinlich hat Befruchtung mit diploiden Sorten die Hauptrolle gespielt, und in dem Falle sind die Tetraploiden aus Verbindung triploider, unreduzierter Eizelle × haploider Pollenzelle entstanden. Dies ist um so mehr wahrscheinlich als JOHANSSON (1937) aus Kreuzung *Boskoop* (triploid) × *Filippa* (diploid) in der Tat schon eine tetraploide Pflanze bekommen hat.

Ob die Sorte *Boskoop* zur Bildung unreduzierter Eizellen besonders geneigt ist, wird sich vielleicht aus fortgesetzten Untersuchungen mit einer gewissen Wahrscheinlichkeit zeigen.

Die Untersuchung zeigt jedenfalls, dass bei der Sorte *Boskoop* Tetraploiden bei grossem Material ziemlich leicht darzustellen sind.

Durch Pfropfung von Knospen der jetzt wachsenden jungen Tetraploidpflanzen auf besonders geeigneten Grundstämmen (u. a. *East Malling N:r 9*) werden hoffentlich die Tetraploiden in wenigen Jahren zur Blüte gebracht werden können, wonach die absichtliche Darstellung des erwünschten grossen triploiden Auslesematerials stattfinden kann.

Bei dieser absichtlichen umfassenden Züchtungsarbeit ist nun ausser der Haltbarkeit des Obstes (nebst allen anderen wichtigen Eigenschaften wie Ertrag, Grösse, Geschmack und übrige Beschaffenheit der Früchte, Resistenz gegen Krankheiten, Kälteresistenz im Klima Schwedens u. s. w.) nunmehr noch ein zweites wichtiges Moment besonders in Betracht zu ziehen, nämlich der C-Vitamingehalt des Obstes. Nach den Untersuchungen von CRANE und ZILVA (1931), GÖTHLIN (1935, 1936) und JOHANSSON (1936) sind die Unterschiede an C-Vitamingehalt zwischen verschiedenen bekannten Apfelsorten (unter etwa denselben äusseren Verhältnissen angebaut) ganz erstaunlich gross (vgl. Fig. 7). Teilweise und wahrscheinlich sogar sehr stark werden diese Unterschiede u. a. von der Triploidie mitbestimmt. In dem mir augenblicklich zugänglichen Untersuchungsmaterial (durch gewisse komplettierende Untersuchungen im Svalöfer-Chromosomenlaboratorium, die ich Herrn Dr. MÜNTZING verdanke, ergänzt) ist der C-Vitamingehalt bei den in Fig. 7 dargestellten 6 Triploiden durchschnittlich etwa doppelt so hoch wie bei den untersuchten 15 Diploiden. Die genauen Mittelzahlen des C-Vitamingehalts in JOHANSSONS Untersuchungen (1936) sind: 6 Triploide $23{,}1 \pm 2{,}34$ Mg. pro 100 Gr., 22 Diploide $11{,}5 \pm 2{,}38$ Mg. Kein

Zweifel kann somit bestehen, dass die bis jetzt untersuchten Triploiden *durchschnittlich* einen höheren, wahrscheinlich sogar viel höheren C-Vitamingehalt als die untersuchten Diploiden besitzen. Schon MÜNTZING (1936 a, S. 367—368, 1936 c) hat im damals vorliegenden Material auf einen höheren C-Vitamingehalt der Triploiden die Aufmerksamkeit gelenkt.

Fig. 7, der von Bureaudirektor SONESSON organisierten Ausstellung

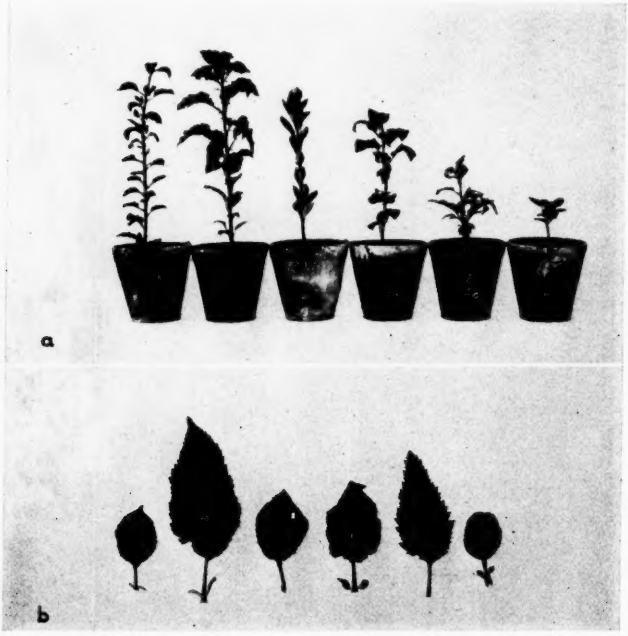


Fig. 5. Auffällige Varianten aus *Boskoop*; a) Pflanzen, b) Blätter der entsprechenden Pflanzen.

»Vårt dagliga bröd» (Stockholm) entnommen, zeigt nun aber auch, dass der C-Vitamingehalt bei verschiedenen Diploiden (sowie auch Tripoiden) ganz ausserordentlich stark schwankt. Dass das importierte Obst so besonders geringen C-Vitamingehalt aufweist, ist offenbar in erster Linie eine modifikative Erscheinung (wahrscheinlich u. a. durch frühzeitiges Herabpflücken der Früchte bedingt), denn dieselbe Sorte (z. B. *Jonathan*) zeigt — siehe Fig. 7 — etwa sieben Mal höheren C-Vitamingehalt in schwedischen Pflanzungen als beim Importobst. Aber

auch zwischen den in Schweden angebauten Sorten sind sehr bedeutende Unterschiede an C-Vitamingehalt zu sehen, sowohl bei Triploiden als Diploiden. Gewisse Diploiden, u. a. *Gelber Richard* und vor allem *Golden Noble* (von Fil. Kand. G. TOMETORP, Svalöf untersucht und als diploid nachgewiesen), stehen, obwohl diploid, in C-Vitamingehalt sehr hoch, erheblich höher sogar als gewisse Triploiden (wie u. a. *Gravensteiner, Ribston*). Die triploide und diploide Kurve des C-Vitamingehalts

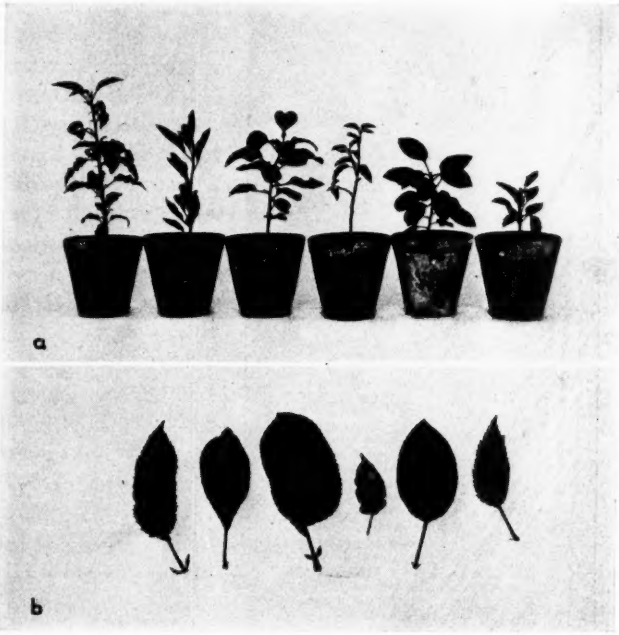


Fig. 6. Auffällige Varianten aus *Blenheim*; a) Pflanzen, b) Blätter der entsprechenden Pflanzen.

greifen m. a. W. sehr stark transgressiv in einander ein, was nichts Auffälliges erbietet, da der erbliche C-Vitamingehalt selbstverständlich (wie alle anderen erblichen Eigenschaften) sehr stark von den Genkombinationen bestimmt wird. Unter solchen Umständen muss man mit Freude begrüssen, dass z. B. *Golden Noble* sich nicht als triploid sondern als diploid erwies, weil dann durch Kreuzung von *Golden Noble* (u. a. besonders vitaminreichen Diploiden) mit den neuen Tetraploiden und scharfe Auslese in der Nachkommenschaft zweifellos die Möglichkeit

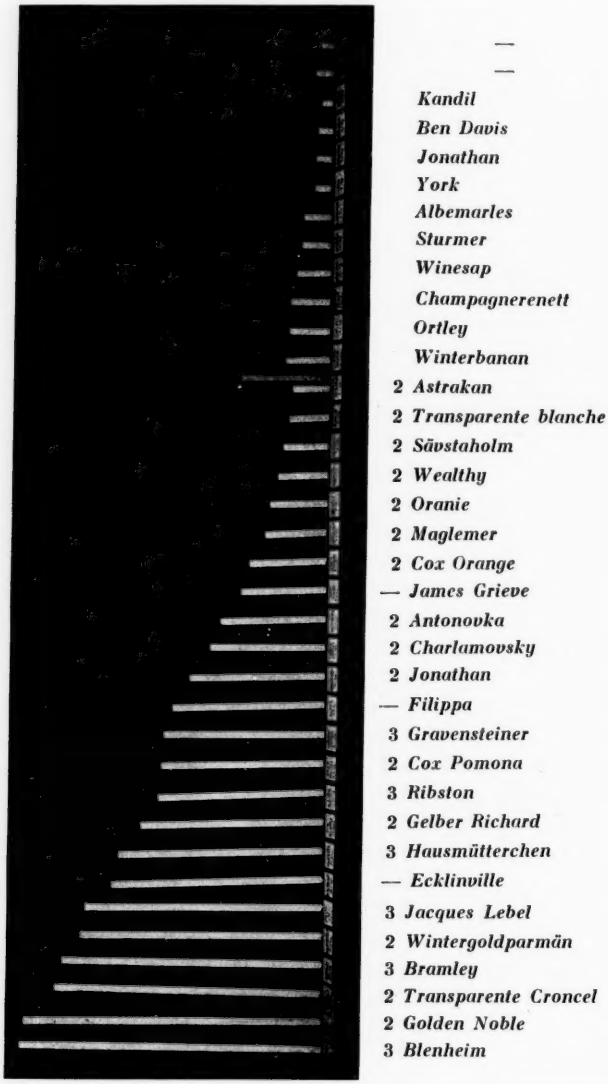


Fig. 7. C-Vitamingehalt (Mg. per 100 Gr. Obst) verschiedener Apfelsorten. Das Bild ist der Ausstellung »Vårt dagliga bröd» in Stockholm 1936 entnommen. Der Drittel oben zeigt den C-Vitamingehalt des Importobstes; der grössere Teil unten zeigt den C-Vitamingehalt verschiedener in Schweden angebauten diploider (2) und triploider (3) Apfelsorten. *Blenheim* enthält 31 Mg. per 100 Gr.

zu einer (wahrscheinlich nicht unbedeutenden) weiteren Steigerung des C-Vitamingehalts über die jetzige Maximalgrenze der Apfelsorten besteht, wenn eine solche Steigerung überhaupt zu erwünschen wäre (was die Ärzte und Ernährungschemiker zu entscheiden haben).

In welcher Weise die Triploidie den Vitamingehalt beeinflusst, lässt sich wohl vorläufig nicht sicher entscheiden. Es ist möglich, dass der höhere Vitamingehalt mit der Spätreife direkt korrelativ zusammenhängt. Auch ist denkbar, obwohl vielleicht weniger wahrscheinlich, dass die Triploidie durch grössere Möglichkeit (als bei den Diploiden) zur Genkombination (vgl. unten) den Boden zur unbewussten Selektion (in Verbindung mit Geschmack?) dargestellt hat, die dann allmählich einen durchschnittlich höheren Vitamingehalt bei den Triploiden im Vergleich mit den Diploiden mit sich gebracht hat. Durch vergleichende Untersuchung in derselben Nachkommenschaft ausgespalteter Triploiden und Diploiden wird diese Frage einmal beantwortet werden können.

Eine für das Klima Schwedens besonders wichtige Frage ist die winterliche Kälteresistenz der angebauten Apfelsorten, und in diesem Zusammenhang entsteht demnach besonders die Frage, ob und wie die Triploidie (bezw. Tetraploidie) auf die Kälteresistenz einwirkt. Vor allem nach den Untersuchungen SCHLÖSSERS (1936), wonach die Polyploidie unter Umständen zu einer Verminderung der Kälteresistenz führen kann, schien es unbedingt notwendig, einschlägige Untersuchungen bei den Apfelsorten nicht zu vernachlässigen. Auf meine Veranlassung hat denn auch Fil. Mag. G. ANDERSSON im Kältelaboratorium Svalöfs im Winter 1936—1937 eine umfassende und sehr genaue Untersuchung einer Reihe diploider (28 Sorten) und triploider (14 Sorten) Apfelsorten durchgeführt, die vorläufig gar nicht für eine durchschnittliche Unterlegenheit an Kälteresistenz der triploiden Sorten den diploiden Sorten gegenüber spricht. Diese Untersuchungen werden jedoch mit noch grösserem Material fortgeführt, wonach die Ergebnisse veröffentlicht werden sollen.

Allerdings ist zu berücksichtigen, dass die Verbreitung der jetzt in Schweden angebauten triploiden Apfelsorten das Endergebnis einer unbewussten Selektion an Kälteresistenz sein kann, und eine völlig einwandfreie Beantwortung der Frage bezüglich des allgemeinen Einflusses der Polyploidie auf Kälteresistenz (ebensowie Vitamingehalt) bei Äpfeln wird folgentlich erst möglich sein durch Vergleich z. B. von neuem diploidem und triploidem (bezw. tetraploidem) Ausspaltungsmaterial derselben Nachkommenschaft. Da nach dem oben Gesagten solches Ma-

terial auch in Schweden jetzt vorliegt, wird die weitere Fortführung der Untersuchung in dieser Richtung bald stattfinden können.

Durch die jetzt dargestellten Tetraploiden sind noch mehrere andere für den praktischen Obstbau wichtige Fragen zu lösen. Für Verkaufsobst sind zu grosse Früchte ein Nachteil, und die grosse Menge jetzigen Importobsts hat auch eine mittlere, so zu sagen »ideale» Grösse. Selbstverständlich muss dann auch die erwünschte Grösse der neuen zu züchtenden Apfelsorten, die das Importobst ersetzen sollen, etwa diejenige des jetzigen Importobstes sein. Da nun die Triploidie, wie sonst, zweifellos auch bei Äpfeln die Tendenz zur Vergrösserung der Früchte mit sich bringt, muss genau darauf geachtet werden, dass die Früchte der Triploiden (bezw. Tetraploiden) nicht zu gross werden, um als beliebtes Verkaufsobst dienen zu können. Für diesen Zweck wären dann die neuen Tetraploiden vor allem mit solchen verhältnismässigen kleinfrüchtigen, sehr wertvollen Sorten wie *Cox Orange*, *Königin Louise* (ev. *Pitmaston Pine*, *Rot. Pigeon*, *Ananasrenett*) u. a. zu kreuzen. Die Steigerung der Fruchtgrösse durch Triploidie wird dann nicht zu weit führen.

Andererseits wird der Züchter auch versuchen, durch Kreuzung z. B. der schon, obwohl nur diploid, besonders grossfrüchtigen Sorte *Signe Tillisch* mit Tetraploiden und Auslese der grossfrüchtigsten Triploiden in der Nachkommenschaft als Kuriosität ein Rekord der Grossfrüchtigkeit zu schlagen.

Besonders spannend wird es auch sein, den praktischen Anbauwert der Tetraploiden selber zu untersuchen. Wenn man eine nicht zu geringe Zahl von Tetraploiden guter Abstammung (in Schweden vorläufig fünf; vgl. oben) und auch von verschiedenen triploiden Sorten dargestellte Tetraploiden bekommen hat, hat man ja eine ganz neue und unter Umständen viel reichere und mehr ergiebige praktische Züchtungslinie bei Äpfeln als früher. Die Tetraploidie mag eventuell schon an und für sich direkt eine gewisse praktische Bedeutung haben; noch viel wichtiger ist aber zweifellos die Möglichkeit zur Bildung weit mehr komplizierter Genkombinationen bei den Tetraploiden im Vergleich mit den Diploiden (und auch Triploiden, die ohnehin durch Überwiegen schlechter Aneuploiden in den Nachkommenschaften bekanntermassen als direktes praktisches Züchtungsobjekt wenig in Betracht kommen). Die Zahl der möglichen Genkombinationen bei Äpfeln wird nämlich erhöht von 3^n bei diploiden Sorten zu 3^{2n} bei tetraploiden Sorten (n = Anzahl Genunterschieden).

Ebensowie auf einem grösseren Grundstück ein grösseres und

schöneres Gebäude aufgeführt werden kann, erbieten die Tetraploiden durch Erhöhung der Chromosomenzahl und damit folgende gewaltige Erhöhung der möglichen Genkombinationen weit grössere Möglichkeiten als die Diploiden (und auch Triploiden) für eine planmässige und erfolgreiche Kombinationszüchtung zu praktischen Zwecken. Die Entwicklung der praktisch wichtigen Eigenschaften (wie Ertrag, Qualität, Resistenz, C-Vitamingehalt u. s. w.) in gewünschten Richtungen durch Auslese in den Kreuzungsnachkommenschaften kann bei den Tetraploiden viel weiter führen. Diesen Weg, d. h. Kreuzung verschiedener künstlich dargestellter Tetraploiden, um verbesserte Genkombinationen zu erreichen, hat bekanntlich schon RANDOLPH (1935) beim Mais betreten.

Auch eine weitere Zunahme der Selbstfertilität ist wahrscheinlich bei den Tetraploiden zu erwarten (vgl. CRANE und LAWRENCE, 1931).

Neben Auslese von neuen triploiden Apfelsorten in oben erwähnter Art, dürfte demnach auch die Züchtung bestmöglicher Tetraploiden, durch Kreuzung verschiedener Tetraploiden mit einander und nachfolgende Auslese in der Nachkommenschaft *ein Zukunftsweg ersten Ranges in der Apfelzüchtung werden.*

Die jetzt gelungene Darstellung tetraploider Äpfel wird auch zur Betretung desselben Weges bei Forstbäumen und anderen Pflanzen weiter stimulieren. Gleichzeitig mit den tetraploiden Äpfeln ist in meinem Material auch jetzt die Darstellung der tetraploiden Espe, aus künstlich ausgeführter Befruchtung triploider Riesenespe (vgl. NILSSON-EHLE, 1936; MÜNTZING, 1936 b, 1936 c) mit gewöhnlichen diploiden Espen, gelungen, worüber demnächst ausführlichere Berichte erfolgen werden.

Bemerkenswert ist, dass tetraploide Wildapfelsorten nachgewiesen sind (NEBEL, 1929). Auch ist eine tetraploide Kulturapfelsorte, *Kola* bekannt, die aus Kreuzung mit einer Wildart stammen soll. Dagegen scheinen die schwedischen Tetraploiden der hier beschriebenen Art, aus triploiden Kultursorten dargestellt, die ersten bekannten zu sein.

Die Versuche zur Darstellung von Tetraploiden aus Triploiden werden beim Institut fortgesetzt und zwar auch mit anderen bekannten Qualitätssorten als die bisher benutzten. Von der Ernte 1937 wird beabsichtigt, u. a. die triploiden Sorten *Gravensteiner*, *Ribston*, *Canada Renette*, eine 1937 als triploid nachgewiesene, bei Vrams Gunnarstorp angebaute spätreife, schöne und haltbare Sorte »*Vramsapfel*» und ev. auch andere triploide Qualitätssorten in die Untersuchungen hineinzuziehen.

Für die sorgfältige praktische Durchführung der umfassenden Versuche bin ich Herrn Assistent C. G. VON SYDOW zu besonderem Dank verpflichtet.

ZUSAMMENFASSUNG.

Zusammenfassend kann gesagt werden, dass die Darstellung tetraploider Äpfel aus triploiden Sorten verhältnismässig leicht zu gelingen scheint, jedenfalls bei der Sorte *Belle de Boskoop*. Die tetraploiden Pflanzen unterscheiden sich von den diploiden Pflanzen durch verhältnismässig breitere und tiefer gezähnte, durchschnittlich auch grössere Blätter, vor allem aber durch die erheblich grösseren, breiteren und stärker gezähnten Nebenblätter.

Die nächstliegende praktische Bedeutung der neu dargestellten Apfeltetraploiden besteht darin, dass triploides Auslesematerial, zur Darstellung im Obstbau erwünschter wertvoller, lange haltbarer u. s. w. triploider Apfelsorten, durch Kreuzung der Tetraploiden mit geeigneten diploiden Sorten jetzt in beliebiger Umfassung dargestellt werden kann.

Auch den Eigenschaften der Tetraploiden selber ist Aufmerksamkeit zu widmen. Durch Kreuzung verschiedener Tetraploiden mit einander und nachfolgender Auslese in der Nachkommenschaft bestehen im Vergleich mit Diploiden viel grössere Genkombinationsmöglichkeiten zur Entwicklung und Steigerung allerlei im Obstbau wichtiger praktischer Eigenschaften. Auf diese Weise wird sich vielleicht durch die Darstellung von tetraploiden Äpfeln eine ganz neue, aussichtsreiche Zukunftslinie in der praktischen Obstbaumzüchtung entwickeln können.

ZITIERTE LITERATUR.

1. BERGSTRÖM, I. 1938. Tetraploid apple seedlings obtained from the progeny of triploid varieties. — Hereditas XXIV, S. 210—215.
2. CRANE, M. B. and LAWRENCE, W. J. C. 1931. Sterility and incompatibility in diploid and polyploid fruits. — Journ. of Genetics XXIV, S. 97—107.
3. — 1934. The genetics of garden plants. — London.
4. CRANE, M. B. and ZILVA, S. S. 1931. The anti-scorbutic vitamin in apples. — Journ. of Pomology IX, S. 228—231.
5. GÖTHLIN, G. F. 1935. Biologiska bestämningar av halten av antiskörbjuggsvitamin (vitamin C; ascorbinsyra) hos 12 av de viktigaste i Sverige odlade äpplesorterna. — K. Lantbruksakademiens handlingar och tidskrift LXXIV, S. 884—944.
6. — 1936. Bestämningar av halten av antiskörbjuggsvitamin hos i Sverige odlade och importerade äpplen. — Sveriges pomolog. fören:s årsskrift XXXVIII, S. 129—138.

7. HEILBORN, O. 1935. Reduction division, pollen lethality and polyploidy in apples. — Acta Horti Bergiani XI, S. 129—184.
8. JOHANSSON, E. 1936. Bestämningar av c-vitaminhalten hos äpple- och päronsorter vid Alnarp 1936. — Sveriges pomolog. fören:s årsskrift XXXVII, S. 306—318.
9. — 1937. Kromosomtal hos plantor av äpple och päron ur korsningar mellan olika sorter. — Ibidem XXXVIII, S. 193—204.
10. MÜNTZING, A. 1936 a. The evolutionary significance of autopolyploidy. — Hereditas XXI, S. 263—378.
11. — 1936 b. The chromosomes of a giant *Populus tremula*. — Hereditas XXI, S. 383—393.
12. — 1936 c. Om kromosomerna och deras verkan hos några trädslag. — Lustgården XVII, S. 1—18.
13. NEBEL, B. 1929. Zur Cytologie von *Malus* und *Vitis*. — Gartenbauwiss. I, S. 549—592.
14. — 1933. Chromosome numbers in aneuploid apple seedlings. — N. Y. St. Exp. Stat. Techn. Bull., No. 209.
15. NILSSON-EHLE, H. 1936. Über eine in der Natur gefundene Gigasform von *Populus tremula*. — Hereditas XXI, S. 379—382.
16. RANDOLPH, L. F. 1935. Cytogenetics of tetraploid maize. — Journ. agricult. research L, S. 591—605.
17. ROSENBERG, O. 1927. Die semiheterotypische Teilung und ihre Bedeutung für die Entstehung verdoppelter Chromosomenzahlen. — Hereditas VIII, S. 305—338.
18. SCHLÖSSER, L.-A. 1936. Frosthärte und Polyploidie. — Der Züchter VIII, S. 75—80.

TETRAPLOID APPLE SEEDLINGS OBTAINED FROM THE PROGENY OF TRIPLOID VARIETIES

BY *INGRID BERGSTRÖM*
INSTITUTE OF GENETICS OF THE UNIVERSITY OF LUND, SVALÖF, SWEDEN

AT the request of Professor NILSSON-EHLE a cytological investigation was carried out last summer at the Institute of Genetics, Svalöf, on a number of apple seedlings from the progeny of the triploid varieties *Belle de Boskoop* and *Blenheim* in order to determine their chromosome numbers. The special purpose of this investigation was, if possible, to obtain tetraploids, which were supposed to have arisen among the material by the functioning of unreduced gametes (cf. NILSSON-EHLE, 1938).

As the material was very extensive — the number of plants amounted to about 4000 — it proved necessary to select certain types for examination. The guiding principle by which this was done was suggested by Professor NILSSON-EHLE, who pointed out that the would-be tetraploids should be looked for among those seedlings which were of a particularly vigorous growth and were characterized by having leaves more or less round in shape, as described in the above-mentioned paper.

Before such a selection was made, a preliminary examination was carried out of a batch of about 70 seedlings picked out at random from the material. Table 1 shows the distribution of the chromosome numbers in different kinds of plants. The designations employed in the table refer to seedlings developed from different types of seeds, Bo 1, 2, 3 denoting *Belle de Boskoop* plants from wrinkled seeds (1, 2, 3 = a little, more, considerably wrinkled), Bl *Blenheim* plants from full, good seeds and Bl 1, 2, as above. In agreement with the data given by CRANE and LAWRENCE (1934) the majority were found to have aneuploid chromosome numbers and to contain plants, as a rule, poorly developed or of a type more or less deviating from the normal (see Fig. 4, third and fourth plant from the left with $\pm$ 38 and $\pm$ 40 chromosomes). Some plants were diploid with 34 chromosomes or approximately diploid and of a normal growth, and a few were triploid

or approximately triploid with 51 and 49 chromosomes respectively, also normally developed and of a somewhat stout appearance. This investigation was undertaken in order to obtain a general idea of the material and is not sufficiently complete to justify any further conclusions.

The task of selecting plants for the search of tetraploids along the above-mentioned line was further facilitated by the fact that Mr. E. JOHANSSON of the Agricultural Institute of Alnarp was lucky enough to find among his material a tetraploid plant *Belle de Boskoop* (3n) × *Filippa* (2n). (Cf. JOHANSSON, 1937). He kindly helped me to pick

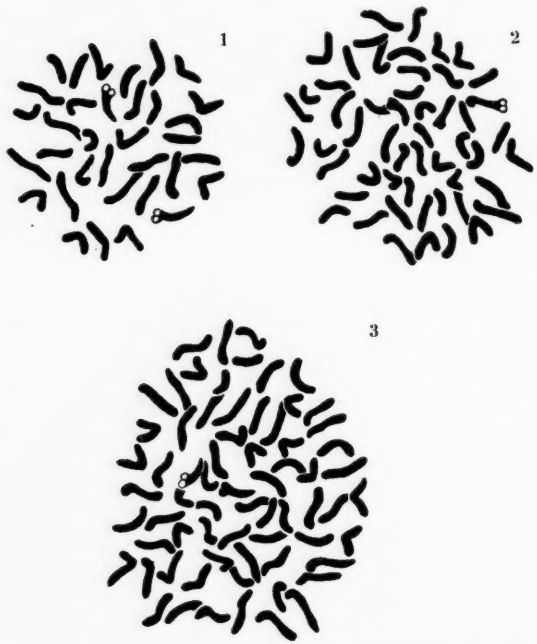
TABLE 1. *Chromosome numbers of apple seedlings from among the progeny of triploid varieties.*

	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	n
Bo 1 ...	1		1		3		1	1								1		1	9
Bo 2 ...			1	2	1	2	2												8
Bo 3 ...					1	3		1											5
Bl.....		1	1	2	1	4		2	1	1	1		2						16
Bl 1.....		1		1	3	1	6		4	2	2			1					21
Bl 2.....	1		1		1	1	1		1		1	1							8

out from among the Svalöf material those plants which resembled in habit the one he had found.

Selections in accordance with the said principle were made on several occasions and the total number of plants procured for investigation was about 70, two thirds of which were of the *Belle de Boskoop* variety and one third of the *Blenheim*. They were all placed in pots in order to yield root-tips for fixation. After a week or two the seedlings of the earlier selections gave plenty of root-tips, the later ones, after a corresponding lapse of time, were less good, the season being then probably too far advanced to be favourable to the growth. About 50 fixations were made in all. As a fixative diluted chrome-acetic-formalin was used and the slides were stained with gentian violet.

In most roots several good metaphase plates were found and the chromosome numbers could be determined fairly accurately in most cases. As a rule counts were made from three roots from each plant.



Figs. 1—3. Somatic plates of diploid, triploid and tetraploid apple seedlings. — Fig. 1, 2n = 34; Fig. 2, 2n = 51; Fig. 3, 2n = 68. — × 3300.

The main part of the selected material was found to be diploid, having 34 or ± 34 chromosomes (Fig. 1) and some were aneuploid with 35, 36, 37 and 41, ± respectively. A few plants were triploid with 51 chromosomes (Fig. 2) or approximately triploid, and two seedlings were aneuploid above the triploid number, having ± 55 and ± 57 chromosomes. (See Table 2 and Fig. 4).

The purpose of finding tetraploids by this method was attained,

TABLE 2. *Chromosome numbers of selected apple seedlings.*

	Chromosome number										n
	34	35	36	37	41	51	52	55	57	68	
Belle de Boskoop.....	27	1	1	2	1	1	1	1	1	4	40
Blenheim.....	6	1			3	1					11

for during the investigation of the selected material four seedlings were found which had a 2n value of 68 (Fig. 4). The plants were all re-fixed for control as soon as they were supposed to be tetraploid and at least six roots were examined from each plant. As the fixations were good in most cases, the chromosomes could be counted without too much difficulty. Some counts gave a somewhat lower value than the exact tetraploid number, namely 65, 66, 67, but several good plates were obtained in which exactly 68 chromosomes could be counted (Fig. 3). The tetraploidy of these four plants, all of which were of the *Belle de Boskoop* variety, thus seems to be beyond doubt, and the expectation of securing tetraploids from the triploid material was fulfilled.

Fig. 4. Apple seedlings from among the progeny of the triploid variety *Belle de Boskoop*. The chromosome numbers are, from left to right, ± 34, ± 36, ± 38, 40, 51, ± 52, ± 55, 68 (Bo 1—71), 68 (Bo 1—54).

Further, it may be mentioned that a number of twin seedlings were examined in respect to their chromosome numbers, the result of which is shown in Table 3. Of the *Blenheim* variety, 16 pairs were obtained and 5 pairs of the *Belle de Boskoop*. The two components of a pair are referred to, as usual, as *a* and *b*, signifying the larger and the smaller plant. The investigated plants — a few *b* seedlings and one pair had died as indicated in the table — were all diploid with one exception — Bo 3 *b* — where the smaller plant was found to be approximately triploid with 51 or 52 chromosomes. In one case — Bl 14 *b* — the smaller plant was distinguished from the other seedlings, which comprised a homogeneous set of normally developed plants, by its dwarfed growth and its disinclination to yield any root-tips, and therefore its

chromosome number could not be determined. Thus no tetraploid seedling has been obtained so far from the twin material investigated, contrary to what has been the case, for instance, in cereals (barley, etc.) and other Gramineæ (cf. MÜNTZING, 1937).

Fig. 4 shows a series of *Belle de Boskoop* plants, the chromosome numbers of which were determined. To the left are a diploid plant (± 34) and one aneuploid close to the diploid number (± 36), both having the appearance generally found among the diploids, tall, rather slender growth and leaves more or less folded together. The next two plants with leaves of a rather deviating shape are aneuploid with a 2n value of ± 38 and ± 40 (cf. above). The small, stout seedling in the centre is a triploid and the one on its right is approximately triploid,

TABLE 3. *Chromosome numbers of twin seedlings of apple.*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Bo *a*	34	34	34	34	34											
Bo *b*	34	—	52	—	34											
Bl *a*.....	34	34	34	34	34	34	34	34	34	—	34	34	34	34	34	34
Bl *b*.....	34	34	34	34	—	34	—	34	34	—	34	—	34	?	34	34

having ± 52 chromosomes. The dissimilarity to the diploids is shown in a stouter growth and the generally rounded shape of the leaves, as appears in the picture of the right hand one of the two plants in question. Next to this one comes a plant which is aneuploid above the triploid number with ± 55. The two seedlings to the right are two tetraploid plants, which plainly display the characters pointed out by Professor NILSSON-EHLE, leaves round in shape and sometimes somewhat recurved and stalks at approximately right angles from the stem.

Measurements of the stomata were also carried out, including diploids, triploids and the four tetraploid plants. The values obtained are shown in Table 4. As was to be expected, in view of the numerous cases recorded of an increase of the cell size in polyploids, the tetraploids, though varying within themselves, gave values considerably above that of the diploids. Of the triploids two instances show similar values, but the third overlaps that one of the tetraploids which shows the lowest mean. The two diploids examined seem to agree. If the diploids prove to be constant with respect to their comparatively low values, this may

be useful as a means by which a preliminary sorting of the material may be affected when further selections are to be made.

As a number of seedlings still remain to be examined among those

TABLE 4. *Length of stomata in diploid, triploid and tetraploid apple seedlings.*

	Length of stomata (units)											n	M ± m
	7	8	9	10	11	12	13	14	15	16	17		
Diploid.....	3	16	35	31	12	2	1					100	$9{,}13 \pm 0{,}11$
»		11	35	39	14	1						100	$9{,}59 \pm 0{,}09$
Triploid		3	13	22	37	20	5					100	$10{,}73 \pm 0{,}12$
»		3	7	29	34	23	4					100	$10{,}79 \pm 0{,}11$
»				16	29	27	21	3	4			100	$11{,}78 \pm 0{,}13$
Tetraploid, Bo 1—54				8	35	37	15	5				100	$11{,}74 \pm 0{,}10$
» , Bo 1—48			1	4	17	31	30	14	3			100	$12{,}39 \pm 0{,}12$
» , Bo 1—71				2	9	21	25	26	14	2	1	100	$13{,}19 \pm 0{,}13$
» , Bo 1—60				1	7	13	30	28	18	3		100	$13{,}43 \pm 0{,}13$

chosen for investigation, and further selections have been made during the autumn, there are prospects of finding more tetraploids.

I wish to express my sincere gratitude to Professor NILSSON-EHLE for having entrusted to me the task of carrying out this most interesting work. I am also greatly indebted to Mr. E. JOHANSSON and to Mr. C. G. VON SYDOW for kind assistance.

Uppsala, November 1937.

LITERATURE CITED.

1. CRANE, M. B. and LAWRENCE, W. J. C. 1934. Genetical studies in cultivated apples. — Journ. of Genetics. Vol. 28.
2. JOHANSSON, E. 1937. Kromosomtal hos plantor av äpple och päron ur korsningar mellan olika sorter. — Sveriges Pomologiska Förenings Årsskrift, 38.
3. MÜNTZING, A. 1937. Polyploidy from twin seedlings. — Cytologia, FUJII Jubilee Volume.
4. NILSSON-EHLE, H. 1938. Darstellung tetraploider Äpfel und ihre Bedeutung für die praktische Apfelzüchtung Schwedens. — Hereditas XXIV.

INHERITANCE OF MAMMÆ IN SWINE, A CHARACTER INVOLVING PARTLY SYMMETRICAL ORGANS

BY *MOGENS PLUM*
THE CARLSBERG LABORATORY, COPENHAGEN, DENMARK

INTRODUCTION.

THE object of this investigation was to study the inheritance of the number of mammæ in swine. Previous investigations on this subject have demonstrated a tendency for the mammæ to be inherited in pairs (WENTWORTH, 1913; PARKER and BULLARD, 1913; NACHTSHEIM, 1924; and SCHMIDT, LAUPRECHT and STAUBESAND, 1936). This tendency is evident from the frequency distributions of the number of mammæ presented by these authors. In all cases it appears that the distributions are not regular, but that even numbers of mammæ appear in excess of odd ones, the ratio of paired to unpaired approximating in some cases 2 : 1. It thus appears that the mammæ in swine are not absolutely paired organs, although there is a tendency to have them develop in pairs. The problem may therefore be considered as one involving a character, the underlying cause of which is a continuous variate capable of expressing itself in whole numbers only. (Naturally one has to assume a whole complex of hereditary and environmental causes rather than a single cause, but this seems to the author to have no influence on the question in hand.) The problem is further complicated by the fact that the character does not express itself to the nearest whole number, the prevalent rule being the formation of even numbers rather than odd ones.

The material used in the present study was collected by the late Professor JOHS. SCHMIDT, formerly Director of the Carlsberg Laboratory, Copenhagen, in connection with his investigations on diallel crossing. This material appeared suitable for a study of the problem in question and at the same time provided a basis for testing a method, which appeared useful in analyzing similar data produced from diallel crossing. The data were collected during the years 1919—1923 at four different breeding centers of Danish Landrace pigs. The records con-

TABLE 1. *Frequency distributions of the number of mammæ in swine as found by different investigators.*

Investigator		Number of mammæ											Percentage even numbers	Remarks
		8	9	10	11	12	13	14	15	16	17	18		
WENTWORTH, 1913 ...	No.		4	195	135	127	33	15						509 Duroc—Jersey pigs, Iowa, U.S.A.
	%		0,78	38,31	26,52	24,95	6,48	2,95					66,21	
PARKER and BULLARD, 1913	No.	1	7	697	1134	2094	962	738	208	111	14	4		5970 unborn pigs of various breeds, Massachusetts, U.S.A.
	%	0,02	0,12	11,68	19,00	35,08	16,11	12,36	3,48	1,86	0,23	0,07	61,06	
NACHTSHEIM, 1924	No.			54	98	218	275	288	49	14	4			1000 pigs of various breeds and crosses, Germany. (Supernumerary nipples included).
	%			5,4	9,8	21,8	27,5	28,8	4,9	1,4	0,4		57,4	
JOHANSSON, 1929.....														96,5 % of 464 Yorkshire (Large White) sows, Svalöf, Sweden.
	%					30,7	38,1	27,7					60,52	
SCHMIDT, LAUPRECHT and STAUBESAND, 1936	No.	1	6	272	323	826	551	637	66	11	1			2694 pigs of various breeds and crosses, Germany.
	%	0,04	0,22	10,10	11,99	30,66	20,45	23,64	2,45	0,41	0,04		64,85	
Present investigation	No.		1	11	43	274	355	701	109	27	2			1523 Danish Landrace pigs, Denmark.
	%		0,07	0,72	2,82	17,99	23,31	46,03	7,16	1,77	0,13		66,51	

sist of 79 groups of full sibs, including altogether 1523 pigs. The size of the full-sib groups varies considerably, ranging from 98 to 4.

SURVEY OF PREVIOUS INVESTIGATIONS.

Table 1 demonstrates the frequency distributions of mammæ found by different investigators. The numbers of pigs with even numbers of mammæ vary from 57,40 % in NACHTSHEIM's data from 1000 pigs of various breeds and crosses in Germany, to 66,51 % in the present data of 1523 Danish Landrace pigs. WENTWORTH's Duroc-Jersey pigs

TABLE 2. *Number and percentage of pigs with paired and unpaired mammæ as found by different investigators.*

Arrangement of mammæ		Investigator			
		PARKER and BULLARD	NACHTSHEIM	SCHMIDT, LAUPRECHT and STAUBESAND	Present investigation
Equal number on both sides	No.	3497	540	1677	983
	%	58,58	54,00	62,25	64,54
Difference of 1 nipple	No.	2323	428		508
	%	38,91	42,8		33,36
Difference of 2 nipples	No.	148	32	1017	30
	%	2,48	3,2	37,75	1,97
Difference of 3 nipples	No.	2	—		2
	%	0,13	—		0,13

and the 2694 pigs in SCHMIDT, LAUPRECHT and STAUBESAND's material have almost the same proportion of pigs with even numbers of mammæ as the present data. The percentages of pigs with 12, 13 and 14 mammæ are given only in JOHANSSON's data from Sweden. The latter include 96,5 % of the 464 Yorkshire sows investigated. The majority of the remaining 3,5 % will probably have either 11 or 15 nipples, and therefore the percentage of pigs with even numbers may not be quite as high as 60,52 %, as recorded in Table 1.

Table 2 shows the number and the percentage of pigs with paired and unpaired mammæ found by different investigators. This table

includes fewer workers than Table 1, because some of the previous studies do not specify whether the mammæ were arranged symmetrically or not. The significance of the difference between these ratios is tested by the Chi square test (Table 3). For each set of offspring is calculated the percentage of asymmetrical offspring $p = \frac{n'}{n} \cdot 100$ and from the totals $\bar{p} = \frac{\Sigma n'}{\Sigma n} \cdot 100$. When $\bar{q} = 100 - \bar{p}$, the formula for Chi square becomes (SNEDECOR and IRWIN, 1933)

$$\chi^2 = \frac{100\ (\Sigma n' p - \bar{p} \Sigma n')}{\bar{p}\,\bar{q}}$$

TABLE 3. *Chi square test of significance of difference in the ratios of paired to unpaired mammæ of swine examined by different investigators.*

Investigator	No. of pigs (n)	No. of pigs with unpaired mammæ (n')	Percentage unpaired (p)
PARKER and BULLARD	5970	2473	41,42379
NACHTSHEIM	1000	460	46,00000
SCHMIDT, LAUPRECHT and STAUBESAND	2694	1017	37,75056
Present investigation	1523	540	35,45634
Total	11187	4490	40,13587

Chi square = 38,7 $P < 0{,}01$

The calculation gives a value of Chi square of 38,7, which for 3 degrees of freedom gives a value of P considerably lower than 0,01 (Table III, FISHER, 1934), indicating a highly significant difference in the ratios of pigs with paired and unpaired mammæ.

OWN INVESTIGATIONS.

The number of mammæ of all pigs were recorded on special forms on the day following birth, cf. Fig. 1. The number of nipples on the right and on the left side were counted and the placings of the mammæ were recorded by checking the corresponding circle on the form. By this method fairly accurate records of the conditions are obtained, provided the mammary patterns are regular and symmetrical. A large number of pigs are, however, born with more or less irregular mammary

patterns and these irregularities were recorded in different ways. As the data were collected many years ago it has not been possible now to verify the accuracy with which the mammary patterns were originally recorded. The present investigation, for this reason, is confined to numbers of mammæ as they appear in one-day-old pigs, and the inheritance of mammary patterns, as studied by WENTWORTH and by NACHTSHEIM, is not considered in this paper.

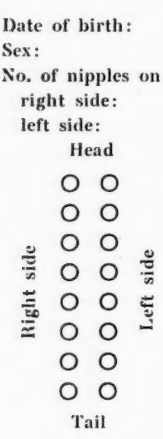


Fig. 1.

The data were analyzed irrespective of sex, since it appeared that there was no significant difference between male and female pigs 1) in the ratio of odd to even numbers of mammæ, 2) in the ratio of paired to unpaired mammæ, 3) in the total number of mammæ. Tables 4 and 5 show the ratios of male and female pigs with even and odd numbers of mammæ together with the ratios of male and female pigs with paired and unpaired mammæ. The sex ratio itself is quite unique, being 761 females to 762 males. The classification of pigs having mammæ in either even or odd numbers is self-explanatory. The

TABLE 4. *Number of pigs with even and odd numbers of mammæ.*

Sex	Number of pigs with mammæ in		Total
	even numbers	odd numbers	
Female	509	252	761
Male	504	258	762
Total	1013	510	1523

Chi square $= 0{,}_{09}$, $0{,}_{80} > P > 0{,}_{70}$

TABLE 5. *Number of pigs with paired and unpaired mammæ.*

Sex	Number of pigs with		Total
	paired mammæ	unpaired mammæ	
Female	493	268	761
Male	490	272	762
Total	983	540	1523

Chi square $= 0{,}_{04}$, $0{,}_{90} > P > 0{,}_{80}$

classification as to symmetry (paired versus unpaired) is made in such a way that all pigs having the same number of mammæ on the right and on the left side are classified as pigs with paired mammæ, even if the mammæ are not located regularly one opposite the other. The group »unpaired mammæ» includes all the remaining pigs where the numbers of mammæ on the right and on the left side do not coincide. Thus a pig with 5 nipples on the right side and 7 on the left side will be grouped according to the first classification in the class »even numbers» and according to the second classification in the class »unpaired». Since differences of two nipples between the two sides are quite rare

TABLE 6. *Analysis of variance of number of mammæ in 1523 one day old pigs.*

Source of variation	Degrees of freedom	Sum of squares	Mean square	z
Between groups of full sibs	78	280,93	3,56	
Within groups of full sibs	1444	1446,95	1,00	
Between sex within groups of full sibs	79	85,67	1,08	0,042
Within sex within groups of full sibs	1365	1361,28	1,00	
Total	1522	1727,88	1,14	

(about 2 % of the cases) the two classifications correspond very closely to each other.

Table 6 shows the analysis of variance of number of mammæ. The determination of the 5 % point of significance is made by FISHER's formula for z (FISHER, 1934, p. 221)

$$z = \frac{1,6449}{\sqrt{h - 1}} - 0,7843\ (1/n_1 - 1/n_2)$$

where $2/h = 1/n_1 + 1/n_2$. For $n_1 = 79$ and $n_2 = 1365$ the z value for the 5 % point of significance becomes 0,1256 demonstrating that no significant sex difference exists in the number of mammæ within groups of full sibs.

INHERITANCE OF ASYMMETRY.

The 1523 pigs originated from four different breeding centers, one of which contributed 1046 pigs, while the three remaining centers con-

tributed only 156, 156 and 165 pigs respectively. The pedigrees of these pigs show that the population in each breeding center may to some extent be regarded as a family group, since each generation is sired by one or two boars only. The percentages of pigs with odd numbers of mammæ were in the four breeding centers 33,8 %, 31,4 %, 25,0 % and 41,2 % respectively (Table 7). The probability that this difference in the ratios of even to odd numbers should be due to

TABLE 7. *Chi square test of significance of differences in the ratios of even to odd numbers of mammæ in swine from four different breeding centers.*

Breeding center	Number of pigs	Number of pigs with odd numbers of mammæ	Percentage odd
A	1046	354	33,84321
B	156	49	31,41026
C	156	39	25,00000
D	165	68	41,21212
Total	1523	510	33,48654

Chi square = 9,8 P about 0,02

TABLE 8. *Chi square test of significance of difference in the ratios of symmetrical to asymmetrical pigs.* WENTWORTH's *data.*

Symmetry of sows	No. of offspring	No. of asymmetrical offspring	Percentage asymmetrical
39 symmetrical sows	340	125	36,76471
18 asymmetrical sows	170	74	43,52941
Total	510	199	39,01961

Chi square = 2,2 $0{,}10 < P < 0{,}20$

random deviations is about 0,02, indicating a significant difference in the ratios of even to odd numbers of mammæ, or what is very nearly the same thing, the ratio of symmetrical to asymmetrical patterns. From this it can be inferred that the degree of symmetry might at least to some extent be due to hereditary factors and consequently subject to some degree of selection.

The problem of inheritance of asymmetry has been studied by WENTWORTH, whose data (Table 8) consisted of 39 symmetrical sows with 340 offspring and 18 asymmetrical sows with 170 offspring. The

symmetrical sows had 36,8 % asymmetrical offspring, while the asymmetrical sows had 43,5 % asymmetrical offspring, from which WENTWORTH drew the conclusion that »while we are justified in assuming a degree of inheritance of asymmetry, we are not yet able to show the same by definite units». A Chi square test shows, however, that the difference in percentage of asymmetrical pigs borne by the two groups of sows is not statistically significant. The conclusion drawn from WENTWORTH's data must therefore be that an indication of inheritance of asymmetry has been demonstrated, although his data do not permit of the determination of this tendency with statistical significance.

Some other figures from WENTWORTH's paper lead to the same conclusion. Among 469 offspring of matings, where only one parent

TABLE 9. *Chi square test of significance of difference in the ratios of symmetrical to asymmetrical pigs.* WENTWORTH's *data.*

Symmetry of mammary pattern in parents	No. of offspring	No. of asymmetrical offspring	Percentage asymmetrical
One parent asymmetrical	469	155	33,04904
Both parents asymmetrical	238	85	35,71429
Total	707	240	33,94625

Chi square $= 0{,}5$ $\quad 0{,}30 < P < 0{,}50$

was asymmetrical, 33,0 % showed asymmetry, while among 238 pigs from matings where both parents were asymmetrical, 35,7 % showed asymmetry (Table 9), a difference which is not statistically significant either.

The present data furnish some evidence on this point. The prevalent custom has been to use breeding animals, in which the number of nipples on the two sides were the same, but several asymmetrical sows and 5 asymmetrical boars have been used for breeding purposes. If the data are grouped according to symmetry of mammæ in the parents, the results are that where both parents have paired mammæ, 34,5 % of the offspring have unpaired mammæ. Where one parent is paired and the other unpaired, the percentage of unpaired offspring rises to 37,4 %, and where both parents are asymmetrical (one asymmetrical boar mated to two asymmetrical sows) the percentage of asymmetrical offspring is 40,9 % (Table 10). Thus there is a gradual increase in the percentage of offspring with unpaired

mammæ, but the Chi square test shows that this difference is not statistically significant. The results obtained from the present data thus corroborate the conclusions which can be drawn from WENTWORTH's data on this subject.

The populations studied by previous investigators show a significant difference in the percentages of asymmetrical pigs. Similar differences are found between the four different breeding centers from which the present data were obtained. This indicates that asymmetry may actually be determined to some extent by hereditary factors. On the other hand, when this hypothesis is tested by comparing offspring of symmetrical and asymmetrical parents within the same population,

TABLE 10. *Chi square test of significance of difference in the ratios of pigs with paired and unpaired mammæ. Own data.*

Symmetry of mammary pattern in parents	No. of offspring	No. of asymmetrical offspring	Percentage asymmetrical
Both parents paired	1018	351	34,47937
One parent paired	454	170	37,44493
Both parents unpaired	22	9	40,90909
Total	1494	530	35,47523

Chi square = 1,5 $0{,}30 < P < 0{,}50$

it is not possible to establish significant differences. If therefore hereditary factors are responsible for some of the asymmetry found it may be assumed that such hereditary factors are only of minor importance. On this assumption, the present data may be analyzed from the standpoint of the number of mammæ by a method which disregards heredity as a factor of asymmetry, at least so long as the analysis is confined to data within such a rather uniform population as that found at a single breeding center. This does not mean, of course, that when a pig, for instance, has 13 mammæ, and consequently is asymmetrical, this asymmetry is not due to hereditary factors. What is meant is only that the method of analysis disregards special hereditary factors, whose sole action is the production of asymmetry, and thus change the phenotype of the individual.

ANALYSIS OF THE DATA FROM STANDPOINT OF THE NUMBER OF MAMMÆ.

The foregoing considerations have led to the conclusion that the factors underlying the determination of the number of mammæ in

swine may be regarded as being continuous in variation, but that there is a preference for expressing the actual number in even numbers or in pairs. This has a marked influence upon the frequency distribution of the number of mammæ. Fig. 2 *a* shows a histogram of the distribution of mammæ in all 1523 pigs. This distribution is a combination of four populations from four different breeding centers and if the distributions from each of these centers are plotted separately (Fig. 3) it becomes evident that they are quite different in shape. *A* and *B* show skewness to the right, *C* shows practically no skewness, while

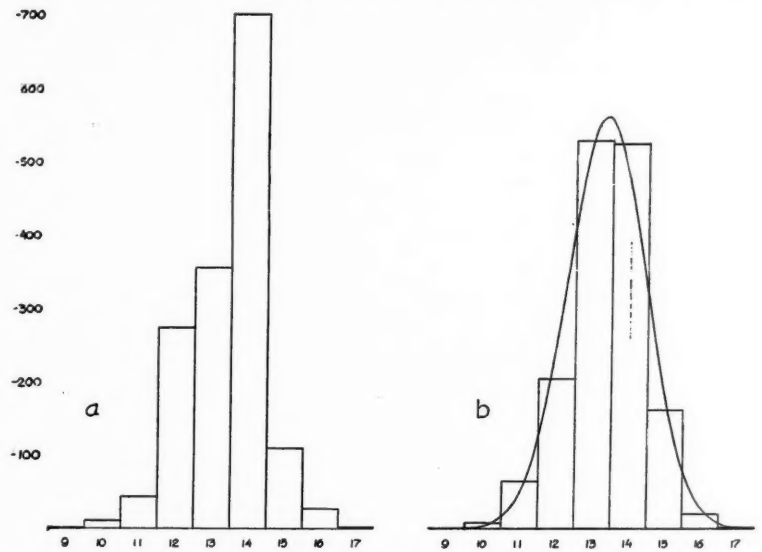


Fig. 2. Histogram showing distribution of the number of mammæ in 1523 Danish Landrace pigs. *a* shows the distribution of the original data, *b* shows the distribution after the numbers in each class have been corrected in such a way that even and odd numbers are made to appear with equal frequencies. The normal curve has a mean of 13,37 and a standard deviation of 1,08.

D shows skewness to the left. Skew distributions are often a result of dominance, but it appears unreasonable that dominance should cause skewness to the left in one population and skewness to the right in another. Moreover, a detailed examination of the distributions shows that the skewness in the distributions is a result of even numbers being much more frequent than odd numbers. The distributions were therefore corrected in such a way that even and odd numbers of mammæ

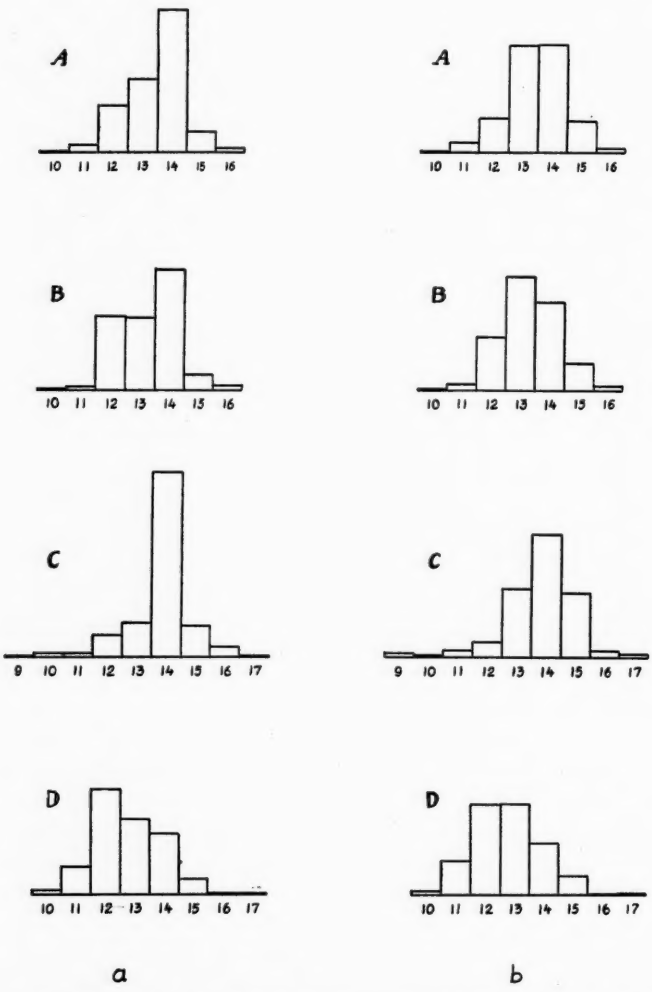


Fig. 3. Histograms showing the relative frequency distributions of the number of mammæ of pigs from four different breeding centers *A*, *B*, *C* and *D*. *a* shows the distributions of the original data while *b* shows the distributions of the corrected figures.

were made to appear with the same frequency, by adding a certain percentage to all classes with odd numbers and subtracting a certain

percentage from all classes with even numbers. In the case of the distribution in Fig. 2 *a*, where 1013 pigs had even numbers of mammæ and 510 pigs had odd numbers of mammæ the correction is made by adding $\frac{761{,}5 - 510}{761{,}5} \cdot 100 = 49{,}31\ \%$ to the odd-numbered classes and subtracting $\frac{1013 - 761{,}5}{1013} \cdot 100 = 24{,}83\ \%$ from all the even-numbered classes. The corrected distribution is shown in Fig. 2 *b*. The correction changes the mean from 13,40 to 13,37 and the standard deviation from 1,07 to 1,08, which is insignificant. A comparison between the corrected distribution and the normal frequency distribution shows that the corrected distribution has an excess of pigs in classes with 13 and especially 14 mammæ, while there is a deficiency in the classes with 12 and 15 mammæ. Since the data show a preference for using breeding animals with 14 and 13 nipples this excess in the classes of pigs with 13 and 14 nipples may be explained as a result of the selection of pigs with the intermediate number of mammæ.

Comparisons of the corrected distributions and the normal distributions made separately for each of the four breeding centers furnished the same general results, although it is evident that some breeding centers have made heavier selection than others. It is very difficult, of course, to obtain any information about the extent to which the different centers have selected breeding animals with 14 nipples, but a comparison of the corrected distributions with the normal frequency distributions seems to furnish some evidence of the fact — which is well known in practice — that this selection is carried out with varying intensity in the different centers.

Having illustrated the method of correction, it only remains to demonstrate what influence this correction may have upon the result of the analysis of the data. The data were originally collected for the purpose of studying the inheritance of number of mammæ by the method of diallel crossing. This method requires that the same sows should be mated to at least two different boars. In this way the generative values of the sows may be determined independently by matings to two or more different boars, and the generative values of the boars may be determined independently by matings to different sows. The present data do not include very many cases of actual diallel crossing, but one case, involving 444 offspring from matings of two boars with four different sows (Table 11), furnishes enough material to demonstrate how the results of the diallel crossing are

materially influenced by the tendency of the number of mammæ to be expressed in pairs. The four sows all had 7 pairs of mammæ, while boar X had 7 pairs and boar Y 6 pairs.

The principle of the method of diallel crossing is that the four possible comparisons of the two boars X and Y should give the same differences in the generative value of the two boars, and that the two possible comparisons of the four sows a, b, c, and d should give the same differences between the generative values of the sows. Table 12 shows the mean number of nipples of the eight groups of pigs resulting from the matings of the two boars with the four sows. The offspring of boar X show higher values throughout than those of boar Y. The

TABLE 11. *Number of offspring from matings of two boars X and Y with four sows a, b, c, and d.*

Boar	Sow			
	a	b	c	d
X	69	97	61	36
Y	49	46	55	31

TABLE 12. *Mean number of nipples of pigs from matings of two boars X and Y with four sows a, b, c, and d. Original figures.*

Boar	Sow			
	a	b	c	d
X.....	13,55	13,62	13,90	13,58
Y.....	13,10	13,24	13,60	13,00
2 (X—Y)	0,90	0,76	0,60	1,16

order of the sows is c, b, d, a in matings with boar X, and c, b, a, d in matings with boar Y. A detailed study of the results shows that in the matings with boar X, the three sows b, d and a have approximately the same value, but that there is a greater difference between these sows when they were mated to boar Y. The result of this analysis shows boar X to be superior to boar Y, and sows c and b to be superior to sows d and a. In general this might be considered a fairly satisfactory result of the analysis were it not for the fact that a correction of the figures appears to give much more consistent results.

The correction was made in the manner illustrated above. A frequency distribution was made for each of the eight groups of pigs, and the frequencies were then corrected by adding to the classes of pigs with uneven numbers of mammæ and subtracting from the classes of pigs with even numbers in such a way that the numbers of pigs with

even and odd numbers became the same. The mean number of mammæ was then calculated on the basis of these corrected frequencies and the results are shown in Table 13. While the differences in the generative values of the boars varied from 0,60 to 1,16 when the uncorrected figures were used, it is now found that the differences between the two boars vary considerably less, viz. from 0,76 to 0,86. The correction has thus made a considerable improvement in the agreement of the four independent tests of the relative breeding values of the two boars. Table 14

TABLE 13. *Mean number of nipples of pigs from matings of two boars X and Y with four sows a, b, c, and d. Corrected figures.*

Boar	Sow			
	a	b	c	d
X.....	13,46	13,62	13,88	13,39
Y.....	13,08	13,22	13,45	12,96
2 (X—Y)	0,76	0,80	0,86	0,86

TABLE 14. *Differences in the relative breeding value of four sows a, b, c, and d, determined by matings to two boars X and Y. The differences are between sows in the vertical column (b, c, and d) and sows in the horizontal row (a, b, c). For each pair of sows, the two independent values obtained from matings with boar X and Y are given.*

	Original figures				Corrected figures		
	a	b	c		a	b	c
b X	0,14			b X	0,32		
Y	0,28			Y	0,28		
c X	0,70	0,56		c X	0,84	0,52	
Y	1,00	0,72		Y	0,74	0,46	
d X	0,06	— 0,08	— 0,64	d X	— 0,14	— 0,46	— 0,98
Y	— 0,20	— 0,48	— 1,20	Y	— 0,24	— 0,52	— 0,98

shows the differences between the breeding values of the four sows before and after correction of the figures. The differences in the breeding values of any two sows are determined independently from matings with the two boars X and Y, and the table is so arranged that an easy comparison can be made between each of the two independently determined differences between any two sows. A considerably better agreement between the results is obtained by the use of corrected figures instead of the original ones.

The method of diallel crossing has received general recognition as a sound method of analyzing data involving quantitative characters.

The fact that the diallel analysis gives considerably more consistent results when the corrected and not the original figures are used, seems to justify the assumption that the number of mammæ in swine is a typical quantitative character, the underlying cause of which is continuous in variation, but whose expression is limited to whole numbers, with a preference of even (paired) numbers rather than odd.

SUMMARY.

The mammæ in swine show a preference of developing in even numbers (pairs) rather than odd. In the present investigation data involving inheritance of the number of mammæ are analyzed by the method of diallel crossing, the original data being transformed by a method by means of which a correction is made for this tendency to develop in pairs. The results indicate that the number of mammæ in swine is a typical quantitative character, showing no dominance, and the underlying cause of which is continuous in variation.

Acknowledgements. — The present study has been made possible by a special grant from the Carlsberg Laboratory, Copenhagen, for which the author wishes to express his appreciation. The data have been placed at the author's disposal by Professor Dr. Ø. WINGE, Director of the Carlsberg Laboratory, to whom special thanks are due for valuable criticism and stimulating encouragement.

LITERATURE CITED.

1. FISHER, R. A. 1934. Statistical methods for research workers. Fifth edition. — London, Oliver and Boyd.
2. JOHANSSON, I. 1929. Statistische Untersuchungen über die Fruchtbarkeit der Schweine. — Zschr. f. Tierzüchtung u. Züchtungsbiol., Bd. 15, pp. 49—86.
3. NACHTSHEIM, H. 1924. Untersuchungen über Variation und Vererbung des Gesäuges beim Schwein. I. — Zeitschr. f. Tierzüchtung u. Züchtungsbiologie, Bd. 2, pp. 113—161.
4. PARKER, G. H. and BULLARD, C. 1913. On the size of litters and the number of nipples in swine. — Proc. Amer. Acad. Arts and Sciences, Vol. 49, pp. 399—426.
5. SCHMIDT, J., LAUPRECHT, E. und STAUBESAND, H. 1936. Untersuchungen über die Vererbung der Trächtigkeitsdauer, des Geburtsgewichtes und der Zitzenanzahl beim Schwein. — Zeitschr. f. Züchtung, B., Bd. 36, pp. 55—100.
6. SNEDECOR, G. W. and IRWIN, M. R. 1933. On the Chi-square test for homogeneity. — Iowa State College Journal of Science, Vol. 8, pp. 75—81.
7. WENTWORTH, E. N. 1913. Inheritance of mammæ in Duroc Jersey swine. — Amer. Nat., Vol. 47, pp. 257—278.

NOTES ON SOME MUTANTS IN PISUM

BY *J. RASMUSSON*
HILLESHÖG, LANDSKRONA

INTRODUCTION.

IN the genetic research work in *Pisum*, which the author has been carrying on since 1918, occasionally new types have occurred beside the segregating types. Those new types have generally been interpreted as having been caused by *gene mutation*. Since 1928 all such mutants or suspected mutants have been taken care of, and as far as possible their genetic behaviour has been controlled. Some of the aberrant types investigated have not been inherited but others have been caused by definite gene differences. The mutants, found since 1928, belonging to the last mentioned group will be described in this paper.

The research work in *Pisum* has demonstrated several linkage groups, but still the number of »good» genes is too small to allow the making of chromosome maps. Mainly because of the want of more good genes in *Pisum*, it has been considered convenient to publish these mutant genes already now, in spite of the fact that not all of them are thoroughly investigated. The main purpose of the publication is, in fact, to place this research material at the disposal of investigators of linkage in *Pisum*.

The material used for the investigations mostly comprised progenies from the crosses used for other research work by the author. The parent material of these crosses has been described earlier (RASMUSSON, 1927). One mutant, however, was found in breeding material of the Swedish Plant Breeding Association at Svalöf. Three other mutants have been received from Mr. ERNST NILSSON. Two of the mutants appeared in X-rayed material.

Until 1934 the investigations were carried out at the Genetic Department of the University of Lund, and from 1935 they have been carried out at the Swedish Sugar Association's Beet Breeding Institute, Hilleshög.

GENE SYMBOLS USED.

The gene symbols in general use among *Pisum* investigators have been named by quite a number of authors working independently.

The result is that there is very little conformity in those symbols. When several genes affecting one character (for instance, flower colour, length, etc.) are known the memorizing of the symbols would surely be facilitated if genes with their main effect in one character had similar symbols discriminated by an index or a suffix. For the old genes a general agreement between the leading *Pisum* investigators would be necessary, but new genes can immediately be given symbols determined on the principle mentioned.

The new genes described below are given symbols as follows: all genes mainly affecting the chlorophyll have been given the symbol *ch* with an index letter designating the specific gene, all genes mainly affecting length of internodes and plant are symbolized by *l* with an index letter.

It may be mentioned further that in this paper the symbol + is used for the »normal dominant» type. The type carrying all known dominant genes should thus be considered the absolute + type. A specific genotype should be characterized by its recessive genes. In the special cases where only one gene is discussed the + symbol is still used to designate the dominance of the gene in question.

The status of the *Pisum* genotypes treated below is characterized by the following genes (symbols = MATSUURA, 1933, where nothing else is mentioned):

a, a_r, *b*	flower colour
j, *h*, *z*, *oh*, *m*, *mp*, *f*, *pl*	seed coat colouring
d(*dw*)	leaf axil colour
gp, p_1	pod colours
g, *i*, *o*	cotyledone colour
r	cotyledone surface
s	chenille
le	internode length
fa	umbellatum type
bl, *w*, wl_o	wax (NILSSON, 1932—33)
st	form of stipules
tl	tendrils
k	wing form
p, *v*	pod texture
n	thickness of pod
fs	female sterility
uni	leaf type (LAMPRECHT, 1933)

In the following pages the type dominant in all the genes mentioned in this list is designated +, and in the descriptions of the types mention is made of the genes in the list in which the genotype described is recessive.

CHLOROPHYLL MUTANTS.

It is well known that chlorophyll mutants represent the most common type of mutants in plant material. — In the author's material, too, chlorophyll mutants occurred much more frequently than other types.

In the description below the chlorophyll mutants have been distributed according to their general colour.

MUTANT ch_a.

The ch_a plants show already in sprouting a light yellowish green colour. When the first leaves develop they are definitely of a lighter colour than the + leaves, but still markedly more green than yellow. Two—three weeks after sowing, the colour of the ch_a leaves become mottled green and bright yellow. During the next two weeks the chlorophyll of the already developed leaves is destroyed more and more and the 2—3 new leaves, which appear in this period, have from the very beginning a lighter green and more yellowish colour than the first leaves had. The mottling appears sooner in the new leaves than in the old ones. From 4—6 weeks after sowing the ch_a plants die, always beginning with the first developed leaves.

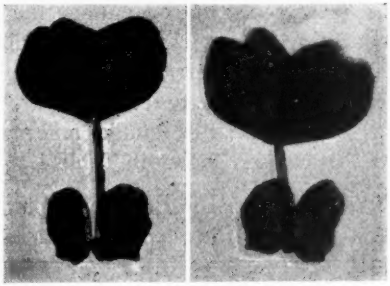


Fig. 1. + (left) and ch_a (right) leaves.

The genotype of the ch_a material is: *m mp pl* p_1 *PV—pv*.

Very great quantities of ch_a material were grown in some years. In that way definite differences in the life-length of the ch_a plants belonging to different families were observed. By selecting for propagation families with comparatively long-living ch_a plants, attempts were made to increase the life-length of the ch_a type. This work has not yet been concluded but we get the general impression that it may be possible to increase as well as decrease the life-length of the chlorophyll defective type by selection acting upon a group or groups of

modifying genes. In no case, however, has it been possible to breed a viable ch_a type and there seems to be no hope of finding one. It might be mentioned, however, that a new mutant (ch_l) appeared in 1933 in the ch_a material. That mutant is at least semi-viable and can by special care be made to produce viable seeds.

The comparatively large amount of chlorophyll in young ch_a plants seemed to make it worth attempting to bring ch_a plants to flower under special care. Several such attempts have been made, *i. e.*, planting them in pots in green-houses and regulating the amount of light, moisture and temperature in different ways. Still, in no case has it been possible to induce the ch_a plants to flower.

THE ORIGIN OF ch_a.

The type was first observed in an F_4 family of the cross *St* × *Gd*. Before that the parent lines had been grown as pure lines for several years, 200—1000 plants of each line being cultivated every year. After the occurrence of the mutant the parent lines have been continued, each year (except 1931 and 1936) about 200 plants of each being grown. No hereditary aberrant types (except in *St* after X-ray treatment) have been found in the parent lines.

The number of families and plants grown in successive generations of this cross is shown in Table 1.

TABLE 1. *Number of single plant progenies and number of plants grown in successive generations of the cross St × Gd.*

Year	Generation	Number of families	Number of plants
1926	F_2	4	1000
1927	F_3	164	2500
1928	F_4	78	1500
1929	F_5	92	2700
1930	F_6	14	300
1932	F_7	265	5300
1933	F_8	270	5500
1934	F_9	4	100
1935	F_{10}	47	2000
1937	F_{11}	25	1000
Total.....	—	963	21900

The ch_a type was first observed in an F_4 family in 1928 (1358/28) derived from one F_3 plant of 1927 (186[I]/27 — pl. 5). 1358/28 segre-

gated 14 + : 8 ch_a. Since the germinating and young plants were frequently and thoroughly observed in 1927, as well as in 1926, there is no chance of a chlorophyll deficiency having been overlooked in those years. This is in fact true of the entire *Pisum* material grown in 1926 and 1927. Thus it is fairly certain that the type did not occur in the author's material before 1928, and this in turn furnishes strong evidence that its appearance is really caused by a mutation $Ch_a \rightarrow ch_a$ in the parent plant of 186[1]/27 — pl. 5.

THE + ch_a SEGREGATION.

The ch_a type has been used in some investigations on the effects of heterozygosity (to be published later) and there is therefore an abundant material for determining its segregation.

Table 2 gives the segregation figures of ch_a. It is obvious that ch_a gives a monofactorial segregation. The main proof of this is the distribution of homozygotes and heterozygotes, which is very definitely established as 1 : 2, proving that the gametic ratio of + : ch_a is 1 : 1 at fertilization. The segregation of + and ch_a zygotes shows a marked deficiency of ch_a with a deviation from expectation of $0{,}121 \pm 0{,}0151$. The cause of this discrepancy must be looked for in the ch_a zygotes themselves, since it has been established that the gametes are normally distributed.

TABLE 2. *Segregation of* ch_a.

Year	Number of progenies			Number in segregating progenies			
	segregating ch_a	constant green	constants pro 3	+	ch_a	ch_a pro 4	± m
1928 ...	—	—	—	14	8		
1929 ...	5	3	1,13	97	32	0,99	0,129
1930 ...	10	5	1,00	318	80	1,80	0,087
1932 ...	143	83	1,10	2868	857	0,91	0,049
1933 ...	3141	1536	0,985	5253	1444	0,86	0,037
1934 ...	1339	775	1,100	76	19	0,80	0,178
1935 ...	32	16	1,00				
1937 ...	13	7	1,05	412	111	0,77	0,128
Total ...	4683	2425	1,023 D/m = 1,37	9038	2551	0,879	0,0151

In the years 1930 and 1932 the germination of homozygotes and heterozygotes in the soil was determined. Altogether about 600 plants with 17000 seeds were investigated. In 1930 the germination percentage

of homozygotes was $85{,}41 \pm 0{,}653$ and of heterozygotes $84{,}00 \pm 0{,}461$; diff. hom.-het. $= +1{,}41 \pm 0{,}799$. In 1932 the germination percentage of the homozygotes was $87{,}85 \pm 0{,}710$ and of the heterozygotes $91{,}04 \pm 0{,}444$; diff. hom.-het. $= -3{,}19 \pm 0{,}837$. The two years together give diff. hom.-het. $= -0{,}43 \pm 0{,}585$. Thus it seems fairly obvious that there is no general difference in germination percentage between homozygotes $++$ and heterozygotes $+ ch_a$, which implies that the deficiency in ch_a plants cannot be caused by differences in germination power between $+$ and ch_a plants. If the deficiency in the number of ch_a plants were due exclusively to the inferior germination of the ch_a plants there should be a difference in germination between $+$ and ch_a of nearly 16 % and there should then be a difference of about 4 % between the seeds from homozygous and those from heterozygous plants in favour of the homozygotes. Evidently, the figures mentioned above do not even indicate such conditions. Still, they cannot quite decide the matter, because there is always the possibility that the $+ ch_a$ plants are more vital than the $++$ plants, which might easily counterbalance a deficient germination of the ch_a plants and give the same germination to the seeds of the heterozygotes as to those of the homozygotes.

LINKAGE RELATIONS OF ch_a TO p AND v.

The family 1358/28 segregated in plants with parchmented and non-parchmented pods, both genes *p* and *v* segregating. In 1932 the status of the plants with respect to pod parchment and homozygosity for ch_a was determined. The figures for number of homozygotes were weighed for number of observed plants: when the progeny of a mother plant numbered less than 26 without showing any ch_a types it was entered into the addition list of homozygous plants, as the probability figure of its being homozygous and to the list of heterozygotes was added 1—P. Thus a plant with a progeny of 20 plants is recorded as 0,98 homozygotes and 0,02 heterozygotes a. s. o.

A further complication is brought about by the fact that both *p* and *v* are segregating in the material investigated and in some progenies both segregate simultaneously. No account was taken as to which factor was segregating, and the numbers of plants in the single progenies were often too small to decide whether there was a 3 : 1 segregation or a 9 : 7 segregation. Even under these circumstances a linkage between one of the parchment genes and the ch_a gene would be visible in an effect on any measure of association. The figures observed were:

Pod	ch_a	Number observed	Number expected from ratios of alternatives of each character
parchment	++	50,51	51,88
»	+ ch_a	97,49	96,12
no »	++	29,06	27,69
» »	+ ch_a	49,94	51,31

This gives $\chi^2 = 1{,}601$ and $P = 0{,}60$, indicating that there is no significant deviation from the distribution to be expected if there were no linkage between ch_a and *p* or *v*.

MUTANT chr.

The ch_r plants cannot be distinguished from the + plants during the first two weeks after sprouting. At 2—3 weeks the nerves of their already developed leaves become yellow and this colour slowly spreads to the parenchyma. The leaves developing after that time are generally light green in colour from the beginning and continue to show this colour throughout life. At this stage there is no difficulty in distinguishing the ch_r plants and as long as the + plants are in full vigour, *i. e.* until they begin to ripen, the differentiating of the two types offers no severe difficulties. Under good vegetation conditions the ch_r type is viable and will give some few seeds. The genotype of the ch_r material is: *m mp pl* p_1 *a r*.

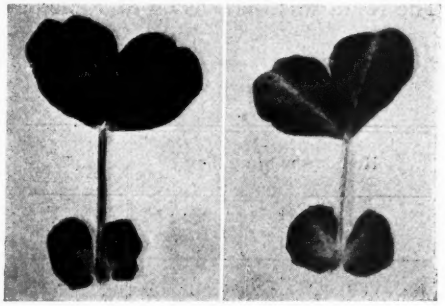


Fig. 2. + (left) and ch_r (right) leaves.

THE ORIGIN OF THE ch_r TYPE.

The ch_r type appeared in X-rayed material of the pure line *St*. Before and after the X-ray treatment, untreated material of that line has been cultivated and observed for 15 years with a total of 2000—3000 plants. In this period no similar type has been found in the *St* line.

In 1933, 200 seeds of the *St* line were treated with X-rays. The

technique of the X-raying was: 105000 volt 1,5 milliampère for 42 minutes at a distance of 35 cm from the anticathode to the surface on which the seeds were placed in a single layer. Half the number of the seeds had been soaked in water for 12 hours before the X-ray treatment. None of the seeds showed any deleterious effects of the treatment, as far as their germination was concerned. The X-rayed seeds were sown the day after the X-raying in the soil used for the *Pisum* cultures. From these seeds 184 plants were grown. None of these gave any signs of abnormality.

In 1934, 27 single plant families were grown. 26 had normal leaf colour (one of these gave a leaf type mutant; see below, page 247), One of the 27 families, *i. e.* No. 112/34, had 18 + plants and 3 with aberrant colour which were described on May 19th as »lighter in leaf colour. Chlorina?».

In 1935, 14 single plant families derived from 112/34 were grown. The result was that shown in Table 3.

TABLE 3. *Homozygotes and ch_r-heterozygotes in the progeny of 112/34.*

Homozygous families		Heterozygous families		
No./35	Number of ++ plants	No./35	Number of + plants	ch_r plants
82	53	90	85	3
83	31	91	9	2
84	27	94	66	2
85	36	Total	160	7
86	14			
87	62			
88	72			
89	83			
92	59			
93	13			
95	43			
Total	493			

In 1937, 15 single plant families derived from 89/35 (++) and 6 single plant families from 93/35 (++?; only 13 plants!) were grown without any of them giving any chlorophyll mutants. The issue of 15 families from 90/35 (+ ch_r) is demonstrated in Table 4.

TABLE 4. *Plant numbers in segregating and non-segregating 1937 families from 90/35.*

Segregating Number of plants		Non-segregating Number of plants
+	ch_r	++
16	1	12
16	2	13
8	5	16
12	1	10
16	2	15
11	2	17
12	5	17
12	2	
Total 103	20	
Pro 4 3,35	0,65 ± 0,156	

In 1937, as well as in 1935, the ratios of non-segregating to segregating and of + to ch_r in the segregating families deviate considerably from the expected monofactorial figures. The material is, however, as yet too limited to allow of either comments or conclusions.

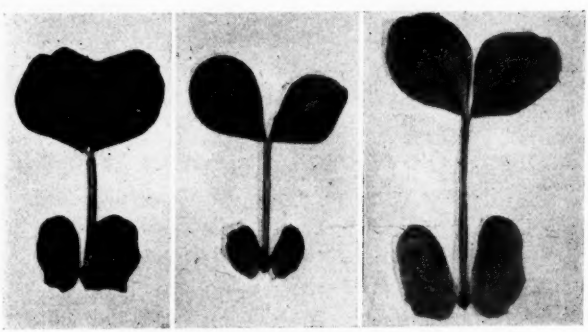


Fig. 3. From the left: +, ch_{c_1}, ch_{c_2}.

MUTANT ch_{c_2}.

A light green, under good growing conditions viable type which immediately after sprouting differs from normally green plants. The genotype of ch_{c_2} is: *m mp pl* p_1 *d*.

ORIGIN OF ch_{c_2}.

Mr. ERNST NILSSON found the ch_{c_2} type in the variety of Solo and has kindly sent material of this type to the author to be included in his collection of chlorophyll deficient types.

In 1935, one segregating family (180/35) was grown in the author's cultures, giving 29 + : 10 ch_{c_2}. Further, one constant ch_{c_2} ch_{c_2} line was grown.

In 1937, five families from 180/35 were grown, giving 3 ++ and 2 + ch_{c_2} families. The segregating families gave altogether 60 + : 16 ch_{c_2} = 3,16 : 0,84 ± 0,199.

Although not much material of this type has been grown, there cannot be any doubt about its being a single gene mutant segregating normally — possibly with a slight deficiency in the number of the recessive type.

MUTANT ch_l.

The ch_l plants sprout with the normal green colour. The second or third leaf is usually a shade lighter than those of the normal plants when developing. The following leaves are light green. When given enough water and not exposed to too strong sunlight the ch_l plants are fully viable, although they are shorter and have a much more slender stem than the normal type. In competition with their normal sister plants, the ch_l plants are only occasionally able to ripen seeds. The type resembles to some extent the ch_r type but has never shown the differentiated colouring of the leaves occurring in ch_r.

The genotype of ch_l is: *m mp pl* p_1 *R—r le.*

ORIGIN AND SEGREGATION RATIOS OF ch_l.

The ch_l type first occurred in 1933 in two families belonging to the ch_a material. In 1926—1930, 352 single plant families with a total of about 7000 plants had been grown in that series without anything like ch_l having been observed. In the two 1933 families 650/33 and 654/33, both segregating ch_a, ch_l plants were found. Both these families originated from one family in 1932 (1587/32), going back to one plant in 1930. Nothing out of the way was observed in 1587/32.

In 1934 some families derived from 650/33 and 654/33 segregated + and ch_l, giving 219 + : 64 ch_l = 3,10 : 0,90 ± 0,13.

In 1935 no record of numbers of plants was made but it was noted that 3 ++ and 7 + ch_l families were found in the progeny of one of the segregating 1934 families.

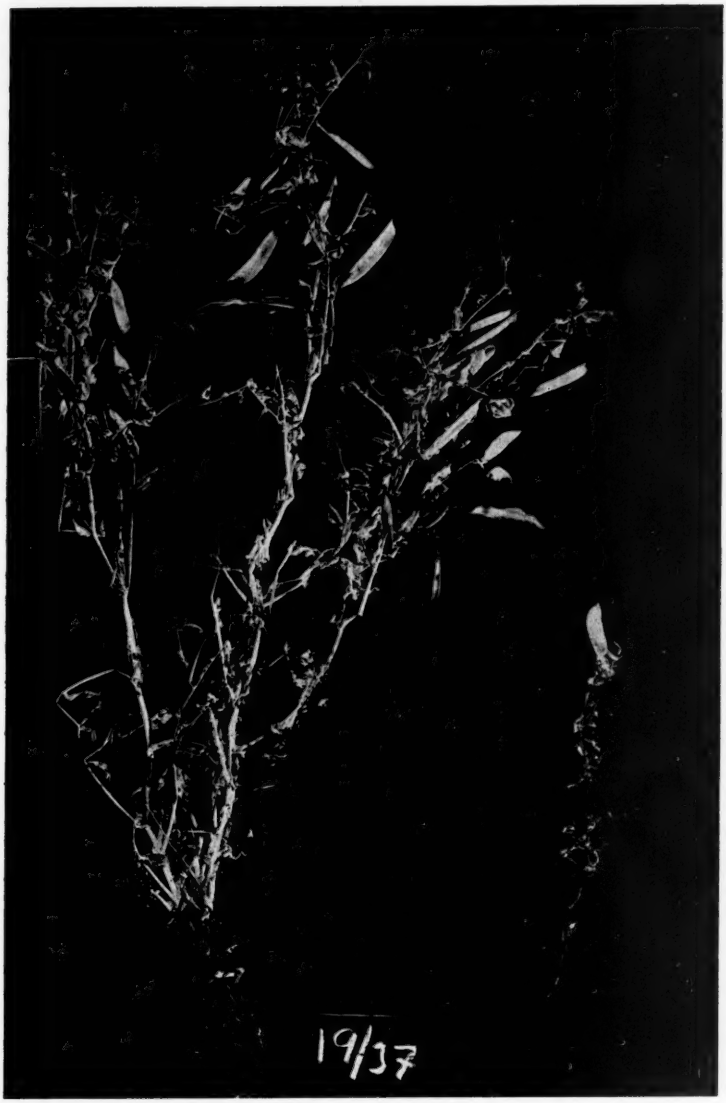


Fig. 4. Ripe plant of normal mother type of ch_1 and ch_1 itself. Grown in the field.

In 1937, 25 families were grown, 4 of which were ++ and 21 + ch_l. The segregating families gave 523 + and 179 ch_l plants = 2,98 : 1,02 ± 0,065.

From the above segregation ratios it is obvious that ch_l is a mutant type segregating monofactorially. Its vitality also seems to be considerably better than that generally shown by chlorophyll mutants in *Pisum*.

RELATIONSHIP OF ch_a AND ch_l.

It has already been mentioned that ch_l was first observed in two ch_a segregating families. The ratios in those families were:

	+	ch_a	ch_l
650/33	38	10	10
654/33	13	3	4
Total	51	13	14

If +: deficient is interpreted as 3 : 1 segregation, the figures give 2,66 : 1,34 ± 0,196 and interpreted as 9 : 7 they give 10,46 : 5,54 ± 0,900, showing that both assumptions are about equally probable.

In 1934 the distributions shown in Table 5 appeared.

TABLE 5. *Segregation of ch_a and ch_l families in 1934.*

Family	Number of plants		
	+	*ch*	ch_l
1205	22	15	0
1206	32	11	0
1208	28	8	0
1207	40	0	13
1209	33	0	10
1210	33	0	10
1212	48	0	14
1213	19	0	5
1215	46	0	12
1211	18	7	7
1214	18	10	5
1216	21	6	8
1217	41	10	16

The ratios from Table 5 calculated on 4 and 16 are:

	+	ch_a	ch_l	m	
ch_a segregating families	2,83	1,17		± 0,161	
ch_l » »	3,10		0,90	± 0,103	
ch_a—ch_l » »	10,10	2,83	3,07	$\chi^2 = 0{,}45$	P = 0,80
+ : (ch_a + ch_l) pro 4	2,33		1,67	± 0,127	
+ : (ch_a + ch_l) pro 16	9,32		6,68	± 0,58	

Further, assuming that + : ch_a : ch_l = 9 : 3 : 4, we should expect the families distributed as:

	expected	found pro 9	
non-segregating	1	0	
+ : ch_a	2	2,1	
+ : ch_l	2	4,1	$\chi^2 = 3{,}575$
+ : ch_a : ch_l	4	2,8	P = 0,30

From these results the most plausible interpretation is obviously that ch_a and ch_l are two independent genes and that Ch_a ch_l and ch_a ch_l give the ch_l type, whereas ch_a Ch_l gives the ch_a type. The evidence cannot, it is true, be considered as quite conclusive, but until the relationship between the genes ch_a and ch_l has been further investigated this might do as a working hypothesis.

MUTANT ch_{c_1}.

The ch_{c_1} plants are, on sprouting, of a light green colour — a typical chlorina in colour. The colour of ch_{c_1} is slightly darker than that of ch_{c_2}. In spite of this ch_{c_1} is not viable. The ch_{c_1} plants die within 4—6 weeks after sprouting.

The genotype of the ch_{c_1} material is: *m mp pl* p_1 *d*.

ORIGIN AND SEGREGATION RATIOS.

This mutant was found in the variety of Solo by Mr. ERNST NILSSON, who has sent the material to the author so as to be kept in culture.

In 1935, five segregating families were grown, giving a total of 56 + : 13 ch_{c_1} = 3,25 : 0,75 ± 0,210.

In 1937, 15 families were grown, giving segregating : non-segregating = 7 : 8 = 1,40 : 1,60 ± 0,365. The segregating families gave 219 + : 60 ch_{c_1} = 3,14 : 0,86 ± 0,104.

Although there seems to be a tendency to too low numbers of ch_{c_1} plants and heterozygotes the results obtained obviously indicate a single gene difference between + and ch_{c_1}

MUTANT ch_g.

The ch_g plants are, on sprouting, as green as their normal sister plants and keep that colour for 3 to 4 weeks. Then the colour of the ch_g plants seems to fade away, changing from light green, yellowish green to yellow in one or two weeks. Shortly after the leaves have become yellow the plants die and all attempts to keep them alive have been in vain.

The genotype of the ch_g material is: *a m mp* p_1 *pl l r le P—p V—v.*

ORIGIN AND SEGREGATION RESULTS.

The ch_g type was found in two F_4 families (123/28, 124/28) descending from the F_3 family 568/27 of the cross *Es* II × *WW* (RASMUSSON, 1927). In F_2 (1926) 423 plants were grown and very carefully observed without any aberrant types being found. In 1927 the observation of the F_3 material was somewhat less careful than in 1926 and in view of the somewhat whimsical nature of the mutant it is possible that the F_3 family 568/27 may have contained some ch_g plants which were not detected. Besides the progeny of family 568/27, about 400 families with about 7000 plants have been grown from the same cross without any aberrant types being observed.

Until 1933 no segregation counts were made, because it was not until 1932 that the behaviour of this mutant became known.

The segregation ratios are given in Table 6.

TABLE 6. *Segregation results of* ch_g.

Year	Number of families		Number of plants in segregating families	
	+ +	+ ch_g	+	ch_g
1933	5	13	902	258
1934	6	7	178	47
1935	9	28	—	—
1937	4	11	243	85
Total	24	59	1323	390
Ratios pro 3(4) ...		0,87 : 2,13	3,089	0,911
Standard error ...		0,190		± 0,0418
t		—		2,13

From Table 6 it is obvious that there is a single gene difference between + and ch_g. The situation resembles in its details that of ch_a, *i. e.* too small a number of ch_g plants but the heterozygotes fully

up to expectation. Further research work will also in this case have to elucidate the cause of the deficient ch_g numbers.

MUTANT ch_h.

The ch_h plants sprout with a yellowish white colour, which later becomes cream yellow. At the age of 3—5 weeks the ch_h plants die. The genotype of the ch_h material is: *m mp pl* p_1 *le p v*.

ORIGIN, SEGREGATION RESULTS AND RELATIONSHIP TO ch_a.

The ch_h type was first observed in family 757/33 of the ch_a series (F_8 of the cross *St* × *Gd*).

During 1926—1932 single plant families with a total of about 7000 plants had been grown, and in 1933 another 270 families with about 5500 plants were grown of this material. Only family 757/33 gave the distinctly cream yellow plants of ch_h and in none of the other families have any similar plants been observed. Family 757/33 gave ch_a types as well as ch_h types in the following numbers 48 + : 5 ch_a : 10 ch_h. 18 of the 48 green plants were continued in 1934, giving 2 ++, 5 + ch_a and 11 + ch_h. The segregation figures for the segregating families were: 174 + : 47 ch_a = 3,15 : 0,85 ± 0,117 and 293 + : 75 ch_h = 3,08 : 0,92 ± 0,090.

In 1935, 91 families derived from 7 segregating 1934 families were grown. The plants were not counted but it was noted that all families descending from + ch_a families either were non-segregating green or segregated + and ch_a and that all families descending from + ch_h families were either constant green or segregated + and ch_h. In no case were ch_a and ch_h found together in one family.

In 1937, 8 families descending from one + ch_h family of 1935 were grown, giving 3 constant : 5 + ch_h and in the segregating families 189 + : 47 ch_h = 3,23 : 0,77 ± 0,114.

In 1934 some crosses were made between + ch_a and + ch_h families. In no case were sufficient F_1 seeds produced from one pair of parent plants to allow definite conclusions to be drawn as to the relations between ch_a and ch_h, although 2 ch_a and 1 ch_h plants occurred in F_1. In F_2 of these crosses some families segregated either + : ch_a or + : ch_h and in no case did the two mutants appear in the same family.

The evidence gathered about ch_h seems to indicate that in part of

the mother plant of family 757/33 the ch_a gene has changed to ch_h, thus making ch_h a multiple allele of ch_a.

Fig. 5. From the left: +, ch_h, ch_d, ch_e.

MUTANT ch_d.

Light lemon yellow. Sprouts white to very light yellow and dies at the age of 3—5 weeks.

The genotype of the ch_d material is: *a m mp pl* p_1.

ORIGIN AND SEGREGATION RESULTS.

This mutant was found by Mr. ERNST NILSSON in a mutated ($n \rightarrow N$) line of the variety Roi des Gourmands.

The segregation results collected are given in Table 7.

TABLE 7. *Segregations of* ch_d.

Year	Number of families		Number of plants in segregating families	
	+ +	+ *ch*	+	ch_d
1933	4	2	27	12
1934	2	4		
1935	6	8	165	48
1937	3	13	92	23
Total	15	27	284	83
Ratio	1,07	1,93	3,09	0,91
m	± 0,219			± 0,091

Although there is a slight deficiency in the numbers of ch_d plants, the ch_d type is evidently due to a single gene mutation.

MUTANT ch_e.

Light yellow with a very faint tint of orange. Sprouts with a very light yellow colour and dies at the age of 3—5 weeks.

The genotype of the ch_e material is: *a m mp pl* p_1.

ORIGIN AND SEGREGATION RESULTS.

The ch_e type was first observed in two F_5 sister families of a cross between the pea varieties Torsdags × Extra rapid. As this material had previously been cultivated only for practical breeding purposes it is not possible to determine when the mutation occurred.

The segregation results are given in Table 8.

TABLE 8. *Segregation results of* ch_e.

Year	Number of families		Number of plants in segregating families	
	++	+ ch_e	+	ch_e
1934	—	—	43	20
1935	6	13	—	—
1937	6	11	358	57
Total	12	24	401	77
Ratio	1,00	2,00	3,36	0,64
m	± 0,236			± 0,079
t				4,6

In 1937 four of the 57 ch_e plants were not self-coloured but chimaeras of yellow and green.

The ratios of the ++ and + ch_e families indicate that the ch_e type is caused by a single gene difference and this is probably true in spite of the rather heavy deficiency in the number of ch_e plants.

LEAF SHAPE MUTANT.

MUTANT »FUNNEL-LEAVED» = ft.

This mutant has been described once before by DELWICHE and RENARD (1926). They gave the following description of it:

»A striking vine variation having funnel-shaped or pitcher-like leaves was discovered by the junior author, in a nursery lot of canning peas of hybrid origin, on the Ashland Branch Experiment Station of the University of Wisconsin. This interesting vine type occurred in a ratio of five abnormal to 27 normal plants, these thirty-two plants being the progeny from a single parent plant. The parent plant seemed to be normal, the seed being wrinkled.

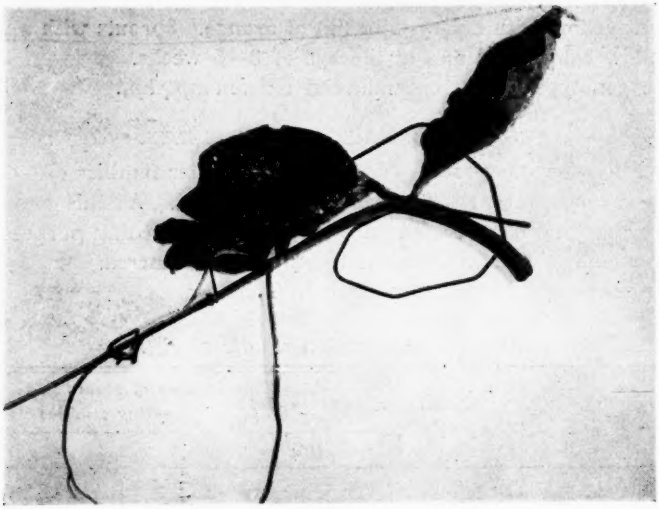


Fig. 7. Funnel-shaped leaf of *fc*.

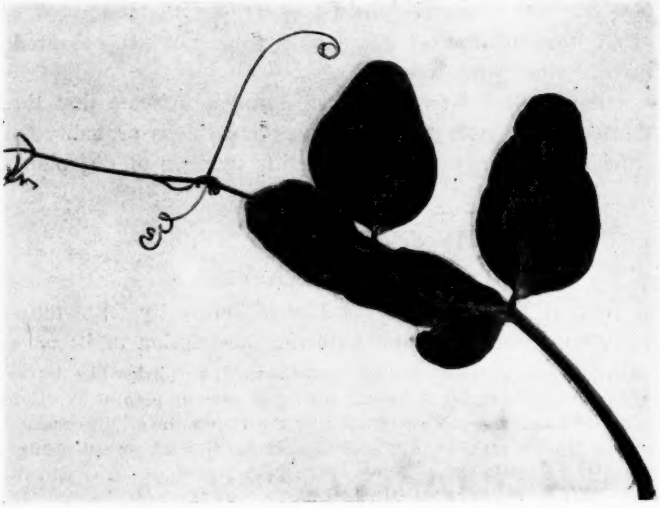


Fig. 6. Normal leaf of *St*.

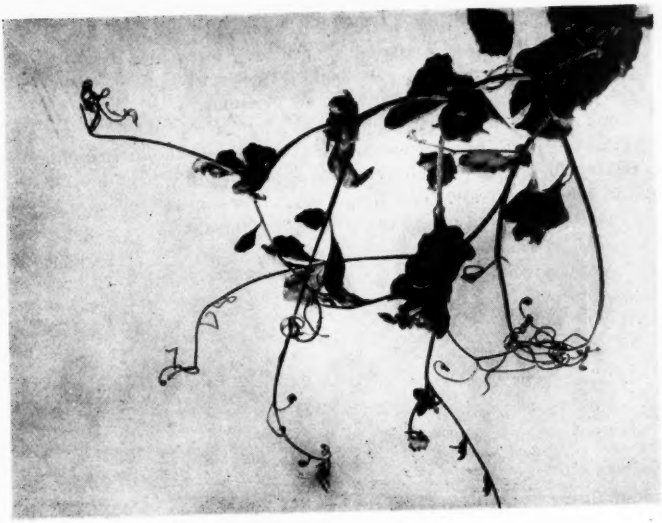


Fig. 9. Top of *fr* mutant of *St*.

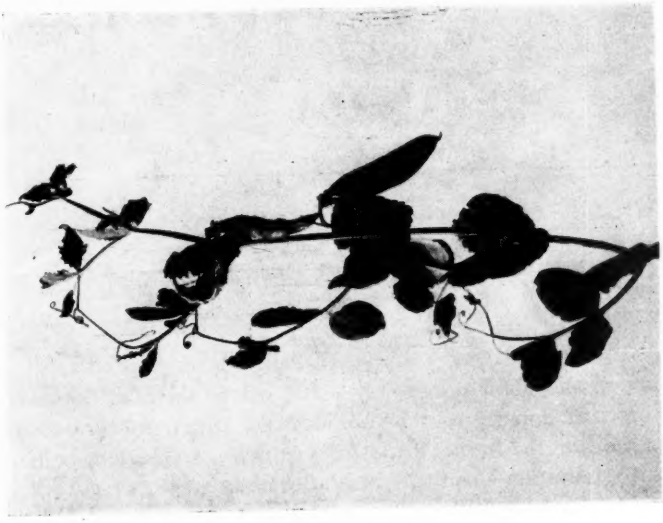


Fig. 8. Top of normal *St* plant with pods.

The leaflets on these abnormal vines were very definitely funnel-like or pitcher-like in shape. On the upper portions of the vine the leaflets were less in number per leaf, being replaced in some cases by profusely branching tendrils. On all abnormal plants tendrils were very abundant. Stipules were of an elongated type. All abnormal plants were sterile, producing no blossoms.

The cause of this aberration apparently may be attributed to some factor change or mutation resulting in a combination to bring about this condition. The factors necessary to produce an abnormal vine could hardly have been present in the original parent or such variations would have shown up in an earlier generation. As the ancestry of the mutant plants was studied individually for several generations, it is known no such variation did occur. So far as known to the writers no such variation in *Pisum* has been reported by other investigators. At least, the literature covered makes no mention of such a find. The lethal effect of the variation itself precludes its propagation.»

The type found by the author fits exactly to that description. The genotype of the author's f_f material is: *a m mp pl* p_1 *r*.

ORIGIN AND SEGREGATION RESULTS.

The funnel-leaf mutant appeared in the X-rayed material (line *St*) which gave the ch_r chlorophyll mutant described above. (For details of the treatment see page 237). About 3000 plants have been grown of the mother line of this mutant without any more mutants of this type being observed.

TABLE 9. *Segregation results of funnel-leaves.*

Year	Number of families		Number of plants in segregating families	
	+ +	+ f_f	+	f_f
1934	—	—	15	5
1935	1	9	234	71
1937	—	—	74	21
Total	1	9	323	97
Ratio			3,08	0,92
M ...				± 0,088

Although the observations, especially concerning the numbers of segregating and non-segregating families, are rather meagre. there is no doubt but that the funnel-leaf type is caused by a single gene having occurred by mutation — in this case after X-raying.

STATURE MUTANTS.

MUTANT »MICRO» l_m.

The mutant »micro» is smaller and more slender than the normal dwarf type of peas from which it originates. Otherwise it is quite normal and it seems to differ only in quantitative measures. Some

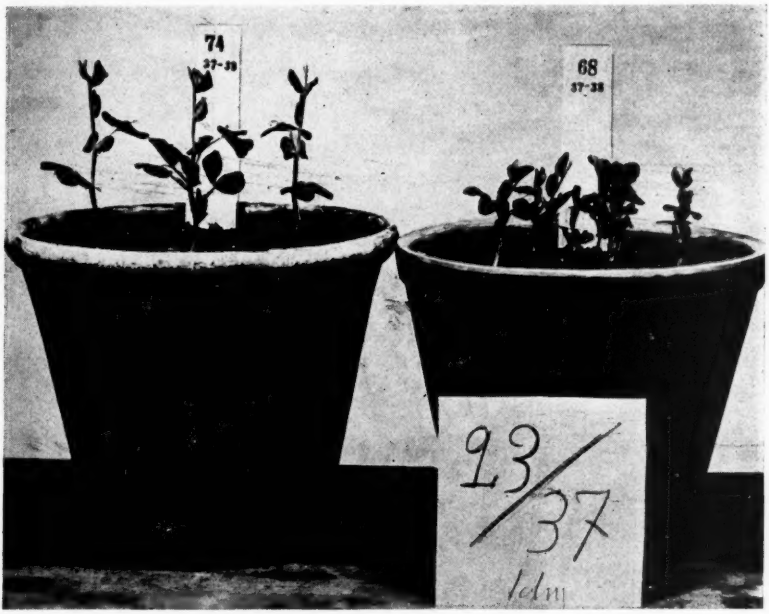


Fig. 10. Normal mother type (74) and »micro» (68) 18 days old, grown in glass-house under electric light.

measurements were made on material grown in the field in 1937 for comparison between »micro» and its normal dwarf mother type, the following averages being obtained:

	Normal dwarf	»micro»
Length of plant in cm.	36,4	12,5
Number of internodes	14,2	10,5
Internode length in cm. (5 middle internodes)	3,46	1,57
» thickness in mm. (5 middle internodes)	3,15	1,78
First flower on internode No.	8,7	8,3
Number of pods	9,7	2,2

	Normal dwarf	»micro»
Pod length in cm.	5,84	3,73
» width » »	1,60	1,17
Numbers of seeds per plant	56,9	12,2
Weight of seeds per plant in grams	9,72	1,68
Average weight of single seed in gram	0,171	0,138

The genotype of »micro» is: *m mp pl* p_1 *le p v*.

ORIGIN AND SEGREGATION RESULTS.

The l_m mutant was first observed in an F_8 family of the cross *Bism* × *Gd* (Cross 11, RASMUSSON, 1927). In F_2—F_7 80 families with

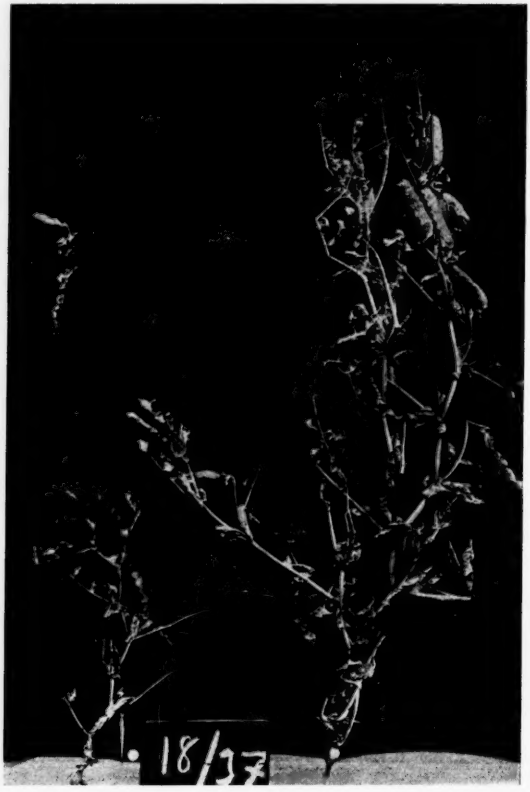


Fig. 11. Left: two »micro» plants; right: normal l_e plant of the mother type of »micro». Ripened in the field.

a total of about 2000 plants were grown and observed. Starting from F_3, the material was selected for early flowering in a purple flowering type. Two F_8 families were grown, one of which was normal throughout, whereas the other gave 23 normal dwarfs: 7 »micro». Since then no segregation counts have been made but the two types have always been markedly different when grown apart.

The »micro» type has evidently arisen by a mutation in the normal l_e type and although the evidence is not by any means complete it

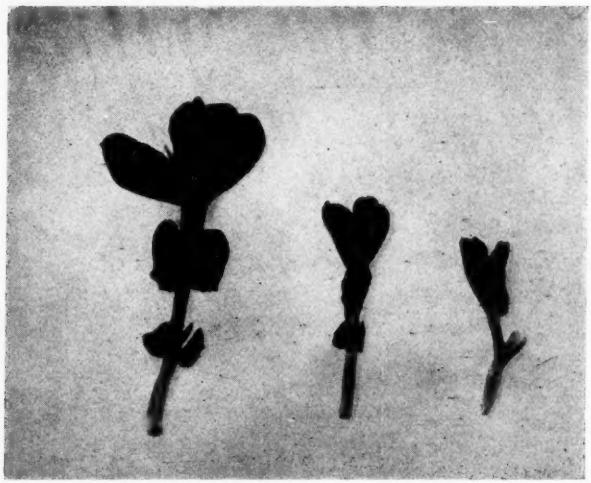


Fig. 12. From the left: normal dwarf, l_m and l_o. 13 days old plants grown in glasshouse under electric light.

seems fairly certain that »micro» differs from the normal dwarf type in a single gene.

MUTANT »ÅNGSTRÖM» l_o.

The mutant »Ångström» differs in size characters from the normal dwarf pea, but it is also distinguished by some morphological characters. It is a very diminutive type, reaching 5—10 cm. in height when the shortest normal dwarfs are 20—30, *WW* 30—40 and *Gd* 40—50 cm. The number of internodes is evidently lower than in the normal l_e type and the internode length seems generally to be less than 1 cm. (normal $l_e = 3$—5 cm.). The leaflets are about $^1/_4$ to $^1/_6$ in surface area compared to normal l_e plants. The leaflets have also an abnormality, *i. e.* on the leaf surface there appear small yellowing spots, which in

fully developed leaves look as if they were sunk down into the parenchyma. When grown in pots in glasshouse the l_o plants flower at about the same time as their parent type. The petals are normally built but small, thus the flower appears to be quite normal. This is not, however, the case, because the edges of the carpel do not fully stick together and thus the ovary is not closed. At the apex of the ovary there is a

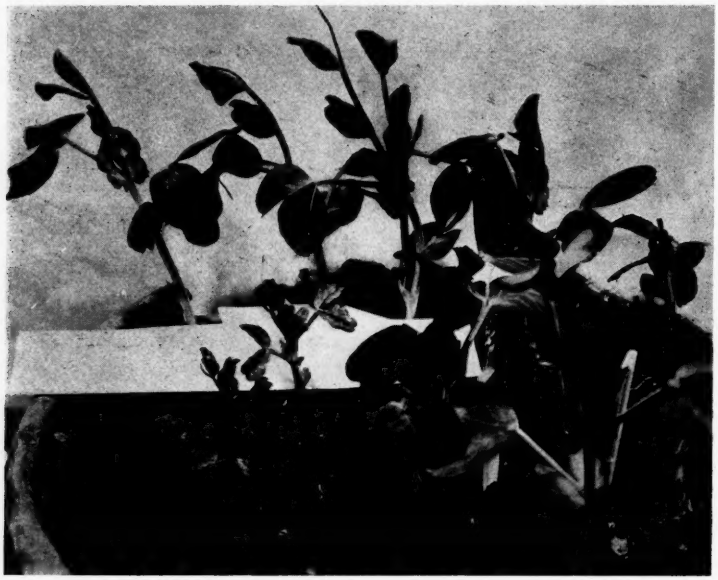


Fig. 13. l_o (small plants just to the left of the centre of the figure) and its normal parent type (the rest of the plants).

small triangular aperture at the morphologically ventral side. Usually one egg protrudes through that aperture on a small stalk. Because of this abnormality the l_o plants do not set seed. The pollen, however, seems to be good — no »bad» pollen grains could be found on examination under the microscope and when used for fertilizing plants of other lines the pollen grains function at least to a certain extent, which is shown by the fact that a few seeds were obtained in such crosses.

The genotype of the l_o material is: *a m mp pl* p_1 *l—i, R—r, le,* W_{lo}—w_{lo}, *Tl—tl.*

ORIGIN AND SEGREGATION RESULTS.

The l_o type was first observed in F_2 of a cross between the acacia type and a l_{wo} line of ERNST NILSSON's (NILSSON, 1932—33). In 1937 six F_2 groups were grown, each descending from one pair of parent plants. One of these groups consisted of 4 families, each descending from a single F_1 plant. These families gave the following results:

Fam.	1890/37	gave	24	normal	0	l_o
»	1891/37	»	34	»	13	»
»	1893/37	»	19	»	0	»
»	1894/37	»	31	»	10	»

There is no doubt that the l_o segregates normally 3 : 1. Further, it is probable that one of the parent plants of the cross was heterozygous for l_o. The actual parent plants of this cross were not marked. Attempts have been made to find the heterozygous mother plant by sowing the stock material from 1934, which ought to contain that parent plant. Due to unfavourable growing conditions the plants were so badly developed that it was impossible to separate the different types. The search for the heterozygous parent plant will, therefore, be continued with the seeds harvested in 1937.

SUMMARY.

This paper gives a list of mutant types in *Pisum* investigated since 1928, their origin and their segregation results.

The following types are mentioned:

ch_a: chlorophyll deficient, not viable; leaves mottled yellow; appeared spontaneously in F_4.

ch_r: chlorophyll deficient, viable; leaf nerves yellowing and finally the whole leaf yellowish green; appeared in a pure line after X-raying the seeds.

ch_{c_2}: light chlorina type, viable; appeared spontaneously in a commercial stock of Solo.

ch_l: slightly chlorophyll deficient, small of stature, viable; starts green, leaves later light green with some yellow; appeared spontaneously in ch_a segregating material (F_8). Together with ch_a segregates probably 9 green : 3 ch_a : 4 ch_l.

ch_{c_1}: nearly green chlorina type, not viable; appeared spontaneously in a commercial stock of Solo.

ch_g: chlorophyll deficient, not viable; starts green, at 3—4 weeks

the leaves become light green, then yellow and the plant dies; appeared spontaneously in F_4 of a cross.

ch_h: chlorophyll deficient, not viable; yellow; appeared spontaneously in ch_a segregating material; probably multiple allele of ch_a.

ch_d: chlorophyll deficient, not viable; leaves yellow with an orange tint.

ch_e: chlorophyll deficient; light lemon yellow; appeared spontaneously in a cross.

f_f: leaflets funnel shaped; viable but sterile; appeared spontaneously in a pure line after X-raying seeds; found once before in U. S. A.

l_m: »micro», stature smaller than normal dwarfs, viable; appeared spontaneously in F_8 of a cross.

l_o: »Ångström», still smaller than l_m, viable but female sterile; leaf surface abnormal; ovary abnormal; appeared spontaneously probably in a pure line.

LITERATURE CITED.

1. DELWICHE, E. J. and RENARD, EARL. 1926. Mutations in the Pea. — Journal of Heredity, vol. 17, pp. 105—106.
2. LAMPRECHT, HERBERT. 1933. Ein *unifoliata*-Typus von *Pisum* mit gleichzeitiger Pistilloidie. — Hereditas, vol. XVIII, pp. 56—63.
3. MATSUURA, HAJIME. 1933. A Bibliographical Monograph on Plant Genetics. — Sapporo.
4. NILSSON, ERNST. 1932—33. Erblichkeitsversuche mit *Pisum*, VI—VIII. — Hereditas, vol. XVII, pp. 197—222.
5. RASMUSSON, J. 1927. Genetically Changed Linkage Values in *Pisum*. — Hereditas, vol. X, pp. 1—152.

CONTENTS.

Introduction 231
Gene symbols used 231
Chlorophyll mutants 233
Mutant ch_a 233
The origin of ch_a 234
The $+ ch_a$ segregation 235
Linkage relations of ch_a to p and v 236
Mutant ch_r 237

The origin of the ch_r type 237
Mutant ch_{e_2} 239
Origin of ch_{e_2} 240
Mutant ch_l 240
Origin and segregation ratios of ch_l 240
Relationship of ch_a and ch_l 242
Mutant ch_{e_1} 243
Origin and segregation ratios 243
Mutant ch_g 244
Origin and segregation results 244
Mutant ch_h 245
Origin, segregation results and relationship to ch_a 245
Mutant ch_d 246
Origin and segregation results 246
Mutant ch_e 247
Origin and segregation results 247
Leaf shape mutant 247
Mutant »funnel-leaved» $= l_f$ 247
Origin and segregation results 250
Stature mutants 251
Mutant »micro» l_m 251
Origin and segregation results 252
Mutant »Ångström» l_o 253
Origin and segregation results 255
Summary 255
Literature cited 256

STUDIES ON THE SIGNIFICANCE OF POLYPLOIDY. II. ORCHIS

BY *O. HAGERUP*
BOTANICAL MUSEUM, COPENHAGEN

SINCE it has been discovered that there is a relation between polyploidy and the ecological behaviour and geographical distribution of a species and that this has perhaps a great influence also on the formation of species in nature (HAGERUP, 1927—1933), polyploidy has been eagerly studied as one of the most important problems of modern biology. The literature available has been so well treated by MÜNTZING (1936) that it will suffice here to refer the reader to his work.

Though the material already at hand for the elucidation of the problems connected with polyploidy is so extensive that it has been treated statistically by TISCHLER (1934) and his school, there still remains much to be desired. Not only are the exotic floras almost unknown in respect to polyploidy, but most of our native species and varieties also stand in need of karyologic investigation. Thus the chromosome number of not a few species is still unknown, and chromosome races especially require to be compared with their respective »main species», while previous counts call for re-examination, etc.

The present work is a small contribution to meet one of these deficiencies within the Danish *Orchis* species, of which I have fixed young flowers, partly taken in nature and partly from Danish specimens planted in the Botanical Garden of the University of Copenhagen. But it is much to be desired that investigators from other regions, especially more southerly countries, should study their indigenous *Orchis* species for purposes of comparison and particularly the varieties and ecotypes.

Already in 1924, FUCHS and ZIEGENSPECK published the first *Orchis* chromosome numbers and stated that in 7 pure species $n = 10$. Of these 7 species I have been able to examine 6, but in none of them did I find the number 10 (but 18, 20, 21, and 40). This is due, among other things, to the fact that the authors have counted chromosome pairs as single chromosomes, as is evident from their drawings and text.

MATSUURA and TIHARU (1935) found $2n = 21$ in the Japanese *O. Fauriei*, and finally HUMPHREY (1932) found $n = 21$ in the *only* two North American species (*O. rotundifolia* and *O. spectabilis*), which differ

greatly from the numerous species of the old world in having rhizomes and roots that hardly show tuberous swellings.

The chief cause of the erroneous counts, however, is doubtless the fact that *Orchis* chromosomes are very difficult to count, both because, in the great majority of cases, they lie densely packed in groups, and also because the largest chromosomes are furnished with constrictions, which makes it hard to tell whether in such cases we are not dealing with small chromosomes lying close together.

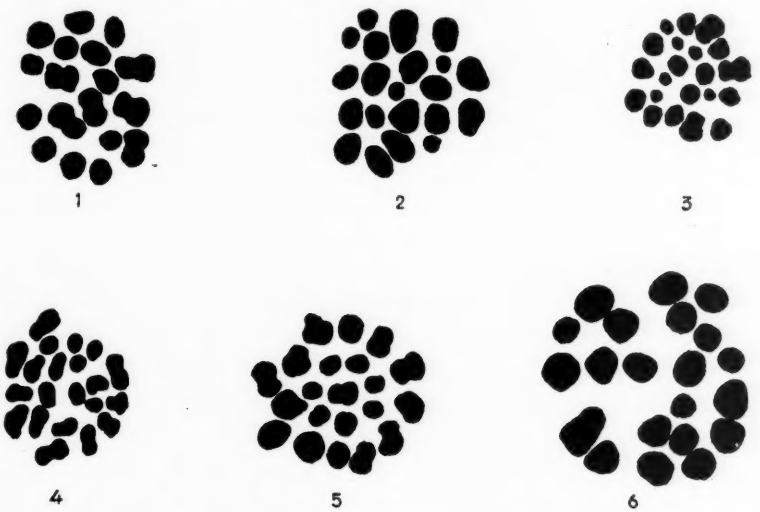


Fig. 1. *O. morio.* n = 18. Metaphase I at meiosis. — Fig. 2. *O. militaris.* n = 21. Metaphase in I division in microspore. — Fig. 3. *O. purpureus.* n = 21. Anaphase I at meiosis. — Fig. 4. *O. sambucinus.* n = 21. Metaphase in I division in microspore. — Fig. 5. *O. masculus.* n = 21. Anaphase I at meiosis. — Fig. 6. *O. ustulatus.* n = 21. Metaphase I at meiosis. — (All figures × 2880.)

To be quite sure, therefore, it will often be necessary to count the phases in which the chromosomes are farthest apart, viz. the *anaphases*, thus, for instance, in *O. masculus*, whose chromosomes lie separated in groups of 2, 3, 4, or 5 in all other phases but the anaphases.

The reduction takes place early, about a month before flowering, and as soon as the floral buds have appeared above the ground they are most conveniently fixed in Carnoy's fixative. They stain well, both according to Heidenhain and Feulgen. It may, moreover, often be of great advantage to examine the first division in the microspore, which

is easier to find than the meiosis itself, because it occurs at a relatively later stage. At any rate the rest of the flower should be removed from the anther, since it is difficult to cut because it contains numerous hard crystals.

Of the 9 species examined here *O. morio* has the lowest number of chromosomes, viz. n = 18 (Fig. 1). About 6 of the chromosomes are exceedingly large, and they appear to be double because they have a constriction in the middle. The remaining 12 chromosomes, on the other hand, are single, spherical, and about equally large.

From these karyologic conditions in *O. morio* the chromosome numbers of all the other *Orchis* species seem to be derivable, partly 1) by division of some of the chromosomes, and 2) partly by tetraploidy. And in addition the association of the chromosomes in groups, which is often easy to see in all the species, would seem to indicate that the number 18, too, is derived in a similar way.

Thus if the nuclear plate (Fig. 3) of *O. purpureus* (n = 21) is compared with the corresponding plate of *O. morio* (Fig. 1, n = 18), it will be seen that 6 of the 21 chromosomes in *O. purpureus* are so small that they seem to have arisen by division of the larger chromosomes, which, indeed, are present now to the number of 15. Something quite similar applies to the closely allied *O. militaris* (Fig. 2) and *O. ustulatus* (Fig. 6), as also to *O. masculus* (Fig. 5) and *O. sambucinus* (Fig. 4), which likewise have n = 21. In all these 5 species there are approximately 1) 6 large »double» chromosomes, 2) 9 medium-sized single, and 3) 6 small spherical chromosomes. These numbers, however, are somewhat variable since it is not always possible to decide whether a chromosome should be regarded as belonging to one or the other order of magnitude, for the picture of the chromsome under observation depends much on the angle from which it is observed.

Thus there occur a number of *Orchis* species, the basic chromosome number of which is 21; and of these *O. ustulatus*, *O. militaris*, and *O. purpureus* are at any rate closely akin. But in addition there occurs yet another series of species, the basic chromosome number of which is 20 (Figs. 7—10), the chromosomes being of three different sizes, just as in the species described above, the 4 smallest chromosomes having perhaps arisen by division of 2 of the larger ones.

As regards polyploidy, the group of species with n = 20 is the most interesting one, because it is highly polymorphous, and because the species are closely interrelated and of common occurrence in quite different localities. In this feature they are the reverse of the species

having n = 21, for polyploidy is not yet known in the latter; they are not very polymorphous and often they will grow only under quite definite external conditions, for instance on calcareous soil.

The two species *O. incarnatus* and *O. latifolius* belong to the 20-series. They are so closely allied that individuals may often be found which cannot, or can only with difficulty, be assigned to one or the other of the two species. And yet they differ cytologically, *O. latifolius* being tetraploid (n = 40, Fig. 8) as compared with *O. incarnatus*

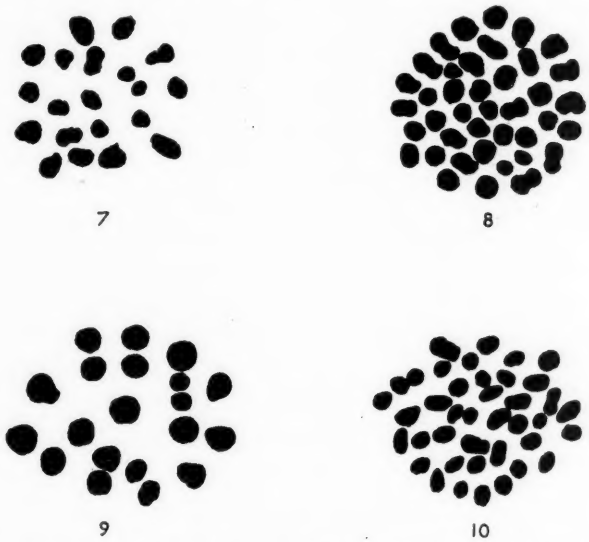


Fig. 7. *O. incarnatus*. n = 20. Anaphase in I division in microspore. — Fig. 8. *O. latifolius*. n = 40. I division in microspore. — Fig. 9. *O. maculatus* var. *Meyeri* (from Møns Klint). n = 20. Metaphase at meiosis. — Fig. 10. *O. maculatus* var. *genuinus* (from Færø Islands). n = 40. Anaphase in I division in microspore.

(n = 20, Fig. 7). These two species afford an interesting example of the fact that polyploidy has not changed the nature of the plant very much; the tetraploid species grows in similar wet meadows to the diploid species, and has about the same range of geographical distribution. But the tetraploid *O. latifolius* is far commoner and more numerous, and flowers about 1—2 weeks earlier.

The most interesting species, however, is *O. maculatus*, because the polyploidy occurring here is quite evident in many respects. The species is of common occurrence and widely distributed from N. Africa to

N. Europe, where it appears in many varieties. Its high degree of polymorphy has been treated, among others, by ASCHERSON and GRÆBNER (1905—07), whose nomenclature I shall employ here.

Diploidy is rare (n = 20, Fig. 9). I have only found it in var. *Meyeri,* which grows in abundance on almost pure limestone under *Fagus* on the cliffs of Møn. This variety, which ranges from France to Scandinavia, but everywhere as a rarity, is easily recognisable by its very broad lower leaves. In addition, the labellum has another shape (Fig. 12) than in var. *genuinus* (Fig. 11). But all the systematic

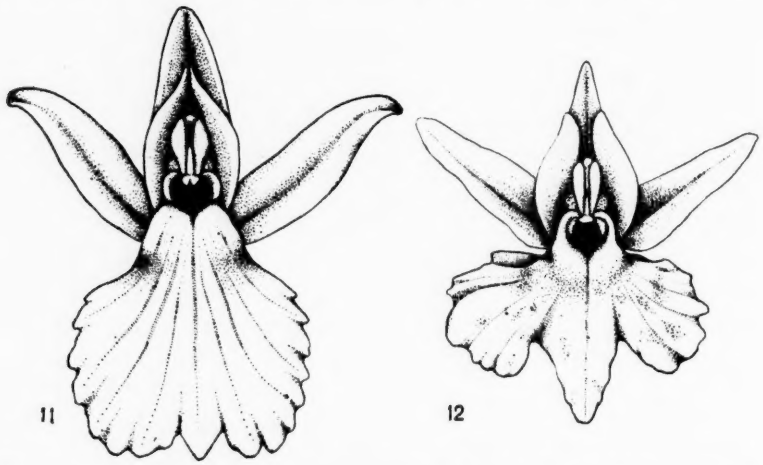


Fig. 11. *O. maculatus* var. *genuinus* (from N. Jutland). (Flower × 5.) — Fig. 12. *O. maculatus* var. *Meyeri* (from Møns Klint). (Flower × 5.)

characters are not very constant; thus a similar marked tripartite labellum as in the broad-leafed var. *Meyeri* also occurs in the very narrow-leafed var. *helodes* in bogs. The cytological conditions show, however, that in spite of this, var. *Meyeri* must be regarded as a separate species.

The great majority of the commoner varieties are, however, tetraploid (n = 40, Fig. 10). Among these I have estimated the chromosome numbers of plants from the Færø Islands and from Denmark, partly from dry and partly from moist localities, and both in feeble and in vigorous individuals of var. *helodes* as well as var. *genuinus*. The result of this investigation is that the tetraploid individuals have by far the greatest ecological and geographical range. None of our

other *Orchis* species are able to grow in such dry localities as the tetraploid *O. maculatus*; but if they are planted in a wet bog they also grow well there. They thrive best on acid soil and do not tolerate lime as does the diploid var. *Meyeri.*

This great vitality of the tetraploid *O. maculatus* manifests itself again in their wide geographical distribution. They extend farthest northward of all our *Orchis* species and are, for instance, very numerous in the Færø Islands and in northern Iceland, where the other species are partly or wholly missing.

Finally, it may be mentioned that there is a peculiar difference in the flowering period, the diploid species flowering early (June) and the tetraploid relatively late, beginning in July; but well on in August many flowers may still be found

There is a slight difference in the size of the different varieties, but curiously enough the tallest variety is the diploid (var. *Meyeri*). It is also more slender; this, however, is doubtless due to the fact that it often grows in shady places (on forest ground).

ROHWEDER (1936) found that polyploidy was especially common in plants growing on calcareous soil; *O. maculatus* var. *Meyeri*, however, affords an interesting example that there are exceptions to this rule too.

SUMMARY.

An investigation of the reduction division of the Danish *Orchis* species has shown the following results:

1. n = 18 in *O. morio.*

n = 21 in *O. ustulatus*, *O. purpureus*, *O. militaris*, *O. masculus*, and *O. sambucinus.*

n = 20 in *O. incarnatus* and *O. maculatus* var. *Meyeri.*

n = 40 in *O. latifolius* and *O. maculatus* var. *genuinus* and var. *helodes.*

2. The polyploidy commonly occurring in *O. maculatus*, as compared with the diploid var. *Meyeri*, showed the following relative characteristics: a) a wider geographical distribution; b) a greater abundance of individuals; c) a capacity to tolerate both dryness, moisture, and cold; d) a capacity to tolerate acidity of the soil; e) a longer and later flowering period; f) a smaller size.

3. Similar differences occur only to a very slight extent between the tetraploid *O. latifolius* and the closely allied diploid *O. incarnatus.*

4. Hence *Orchis maculatus* affords a fresh example of the enorm-

ous influence of polyploidy on the ability of the plants to hold their own in the »struggle for life». Since polyploidy can be produced experimentally by the direct influence of external factors, the origin of new species may also *partly* be due to the direct influence of the environment. (Cp. HAGERUP, 1932, 1933.)

LITERATURE CITED.

1. ASCHERSON, P. und GRÆBNER, P. 1905—07. Synopsis der mitteleuropäischen Flora. III. — Leipzig.
2. FUCHS, A. und ZIEGENSPECK, H. 1924. Aus der Monographie des *Orchis Traunsteineri* SAUT. IV. — Botanisches Archiv. Bd. V. S. 457.
3. HAGERUP, O. 1927. *Empetrum hermaphroditum* (LGE.) HAGERUP, a new tetraploid, bisexual species. — Dansk Botanisk Arkiv, Bd. 5. No. 2.
4. — 1928. Morphological and cytological studies of Bicornes. — Dansk Botanisk Arkiv. Bd. 6. No. 1.
5. — 1932. Über Polyploidie in Beziehung zu Klima, Ökologie und Phylogenie. — Hereditas XVI.
6. — 1933. Studies on polyploid ecotypes in *Vaccinium uliginosum* L. — Hereditas XVIII.
7. HUMPHREY, L. M. 1932. Somatic chromosomes of certain Minnesota Orchids. — Americ. Natural. Vol. 66, pp. 471—474.
8. MATSUURA, H. and TIHARU, S. 1935. Contributions to the idiogram study in phanerogamous plants. I.— Journ. Fac. Sc., Hokkaido Imp. Univ. Ser. V. Vol. V. No. 1.
9. MÜNTZING, A. 1936. The evolutionary significance of autopolyploidy. — Hereditas XXI.
10. ROHWEDER, H. 1936. Die Bedeutung der Polyploidie für die Anpassung der Angiospermen an die Kalkgebiete Schleswig-Holsteins. — Beih. zum Bot. Centralbl. Bd. LIV, Abt. A.
11. TISCHLER, G. 1934. Die Bedeutung der Polyploidie für die Verbreitung der Angiospermen. — Bot. Jahrb. Bd. LXVII, Hft 1, p. 1.

CYTOLOGICAL STUDIES OF ARCTIC GRASSES

BY *KARL FLOVIK*

STATE AGRICULTURAL EXPERIMENT STATION HOLT, TROMSÖ, NORWAY

I. INTRODUCTION.

THE observations put forward in the present work comprise mainly the grass species commonly occurring in Spitsbergen. The chief interest and purpose of this investigation was originally concerned mainly with the viviparous grasses represented here within the genera *Deschampsia*, *Poa* and *Festuca*. But other problems were also given attention and therefore all species available for cytological investigation have been included. As the work proceeded, new problems arose and had to be considered. This refers in particular to the question of the primary basic chromosome number.

In the light of recent investigations carried out by various workers, the *Gramineæ*, with their numerous species and world-wide distribution, have shown themselves to be very interesting objects for cytological studies. But up to the present only a few of very important cultural plants belonging to this family, and then more especially the cereals and their closely related genera, have been subjected to more detailed studies, and as far as these are concerned there is a very extensive and voluminous literature. Investigations of large groups, carried out in connection with systematical, phylogenetic, phytogeographical or ecological problems, embrace essentially the number and size of the chromosomes and otherwise more conspicuous conditions. Investigations of this kind are those carried out by LEVITSKY and KUZMINA (1927), AVDULOV (1928, 1930, 1931, 1933), STÄHLIN (1929) and TURESSON (1930, 1931). The most comprehensive studies of this kind are found in the works of AVDULOV. He tried to find a basis for systematization in the cytological conditions. In an examination of 230 species, distributed among about 100 different genera, this investigator found that the cytological characteristics, which here chiefly apply to the number and the size of the chromosomes, have a very high systematic value. These cytological properties were found to agree very closely with a number of other characteristics of the *Gramineæ*,

such as the anatomical structure of the leaves, the structure of the starch grains, the shape of the first foliage leaves, the geographical distribution and a number of other purely morphological properties.

On the basis of the cytological criteria together with other criteria mentioned, AVDULOV (1931) made revolutionary changes in HACKEL's generally prevailing system. The grass species investigated by him were divided into three karyo-systematic groups. The first of these groups is made up of the sub-family *Sacchariferæ* (HARZ) AVDULOV and is characterized by having small chromosomes and the basic numbers 9 and 10; its geographical distribution is mainly tropical or sub-tropical. The second group, *Festuciformis* AVDULOV, is characterized by relatively large chromosomes, the basic number being 7 or lower and its geographical distribution being chiefly confined to the temperate and polar zones. The third group, *Phragmitiformis* (HARZ) AVDULOV, is also distinguished by small chromosomes but has the basic number 12. The geographical distribution of the group is essentially tropical. The second and third group are again combined into the sub-family *Poatæ* (HITCHOCK) AVDULOV.

Based partly on the cytological findings and partly on other morphological characters, the same author draws up in connection with his karyo-systematic system a phylogenetic scheme comprising the entire family.

In addition to the above-mentioned basic numbers 7, 9, 10 and 12, the basic numbers 5, 6, 11 and 13 also occur. The question thus arises whether all these numbers are to be regarded as primary or whether there are among them also secondary balanced basic numbers. This question is of considerable interest, not the least from a phylogenetic point of view.

AVDULOV considers the *Phragmitiformis* group, with its small chromosomes and the basic number 12, to be the oldest, phylogenetically, of his karyo-systematic groups, and therefore 12 should be the primary basic number in the *Gramineæ*. From certain representatives of *Phragmitiformis* (»the relic group») evolution is thought to have progressed in the direction of an increase in the volume of the chromosomes and a decrease in their basic numbers.

Some of the observations put forward in the present work together with other facts found in the literature give occasion, however, to reconsider the question concerning the primary basic number in this family, for, as will be shown later, the results of the more detailed investigations are incompatible with AVDULOV's hypothesis. Since

AVDULOV put forward his hypothesis, the question does not seem to have subjected to a closer examination, which need not imply, however, that his hypothesis has been generally accepted. Thus, WANSCHER (1934) has suggested that the primary basic number may be 8.

According to the statements of various investigators, polyploidy is very wide-spread in grasses and must be assumed to have been an important evolutionary factor. High polyploid series are frequent, especially in groups with low basic numbers. STÄHLIN (1929) investigated the influence of the degree of polyploidy on the morphological characters of grasses, comparing closely related varieties with unequal chromosome numbers. He came to the result that with an increase in the number of chromosomes there takes place an increase in the size of the cell and thereby in the size of the plant up to a certain limit, beyond which a further increase of the chromosome number brings about a diminution in the size of the cell and of the plant. This is thought to be due to physiological obstructions in that the chromatin mass becomes too large in proportion to the amount of plasm in the cells. In the genera examined, this limit lay between hexaploidy and octoploidy, in *Poa* perhaps a little higher.

As regards vivipary in the form that problem is met with in the grasses under discussion here, there are very few observations from a cytological point of view. STÄHLIN (l. c.) investigated viviparous forms of *Deschampsia flexuosa* and *Poa alpina*. With respect to chromosome numbers these were found to be exactly the same as in non-viviparous forms of the same species, *viz.* in *Deschampsia flexuosa* $2n = 28$ and in *Poa alpina* $2n = 42$. In his investigations of *Festuca ovina* from Scandinavia, TURESSON (1930, 1931) found that the normal, sexually propagating forms were diploids having the chromosome number $2n = 14$, whereas the viviparous forms were triploids and tetraploids and in one case hexaploid — thus having the chromosome numbers $2n = 21$, 28 and 42 respectively. As vivipary was found to be most pronounced in the high polyploid forms there appears to be, according to TURESSON's investigations, a certain relationship between polyploidy and vivipary, so that an increasing degree of polyploidy brings about a higher degree of vivipary. The chromosome numbers of sexually propagating forms and varieties of *Festuca ovina* have, however, been recorded by several other investigators: LITARDIÈRE (1923), LEVITSKY and KUZMINA (1927), LEVITSKY (1928), CHURCH (1929), STÄHLIN (1929), NAKAJIMA (1931) and JENKIN (1933). According to these authors, a beautiful polyploid series can be established. Thus, the numbers

2n = 14, 28, 42, 56 and 70. It is therefore not always true that there is a connection between polyploidy and vivipary in *F. ovina*, for there are highly polyploid non-viviparous forms and varieties. GUSTAFSSON (1935) has also pointed out that in reality it is not always the case, as is generally imagined, that sexual species in apomictic genera have lower chromosome numbers than the apomictics.

In connection with the different views put forward concerning the problem of vivipary it is of vital importance to ascertain whether autopolyploidy or allopolyploidy exists within the viviparous form series. Neither STÄHLIN's nor TURESSON's investigations furnish a satisfactory answer to this question, for the chromosome numbers alone do not provide a foundation for any definite assumptions. TURESSON is nevertheless of opinion that in *Festuca ovina* var. *vivipara* it is more than likely a question of autopolyploidy, and this view seems to be generally accepted. In this investigation special attention has been paid to this important but obscure problem, and for the clarification of this problem as well as many others special chromosome morphological analyses have been employed.

In numerous other cases where the material was suitable for chromosome morphological studies, such studies proved to be of great value and particularly good results were obtained. Mention may here be made of the studies of *Crepis*, originally commenced by NAVASHIN (1925) and successfully continued by various workers (cf. BABCOCK and NAVASHIN, 1930; HOLLINGSHEAD and BABCOCK, 1930; BABCOCK and CAMERON, 1934). Another classical example is MEURMAN's work on *Aucuba* (MEURMAN, 1929 a). Chromosome morphological studies have been carried out also on certain grasses, among others, by MCCLINTOCK (1929), LEVITSKY (1929, 1931), SENJANINOVA-KORCZAGINA (1930), BEADLE (1932), HUSKINS and SMITH (1932), RANCKEN (1934) and NANDI (1936). The various investigations of this kind indicate that the chromosomes in grasses are in general objects which repay study, and for that reason it may be safely assumed that further investigations in this field will bring to light many interesting points. In the present investigation it was also possible to carry out detailed analyses on several species, which may be said to have furnished valuable contributions to the elucidation of the problems involved in the investigation.

While carrying out this investigation I spent quite a long time at the Cytological Laboratory of the State Horticultural Institution, Piikkiö,

Finland. For the interest shown in this investigation by the head of this institution, Prof. O. MEURMAN, in giving me advice and guidance on microtechnical matters and in inspecting my slides and otherwise for discussions concerning various problems, I wish here to express my deep debt of gratitude. I am also greatly indebted to Mr. K. FJÆRVOLL, Director of the State Agricultural Experiment Station Holt, Tromsö, for assistance in many ways in carrying out this investigation. Further, I wish to tender my sincere thanks to Mr. JOHS. LID, Curator of the Botanical Museum, Oslo, who, through his local knowledge of Spitsbergen and the arctic flora, gave me much valuable information and advice and also guidance on the collection of the material and who finally controlled my classification of the material collected. Mr. O. FINNSET, Cand. Agri., Tromsö, rendered valuable assistance during the collection of the material and in making the preparations, for which I am greatly indebted to him.

The collection of the material was facilitated by financial support from »Conrad Holmboe's Research Fund», Tromsö, and the cytological investigations were carried out in their entirety with the aid of grants from »A/S Norsk Varekrigsforsikrings Fond». For the grants made by these two funds I wish to tender my sincere thanks.

II. MATERIAL AND METHODS.

The material was collected by the writer in the summer of 1935, with the exception of the species *Arctagrostis latifolia*, *Arctophila fulva* and *Poa abbreviata*, which were collected by Mr. O. FINNSET in the summer of 1936. This grass material from Spitsbergen was in its entirety collected at Isfjorden, which, owing to its favourable climatic conditions, is one of the richest localities for plants in Spitsbergen. For the discussion concerning the problem of vivipary, I have also included a number of observations on species of *Festuca* from the arctic regions of Norway. Particulars of the localities from which the Spitsbergen material is in each separate case derived will be found in Table 9, p. 328.

All species were brought down to Tromsö in a living state, where they were planted in earthenware pots and otherwise provided with the best conditions of growth. After the plants had made an appreciable amount of growth root-tips were fixed for the purpose of studying the somatic chromosome complements. This was done in order to secure the requisite conditions for obtaining good fixation results, for as

pointed out by MÜNTZING (1935 a) there is a positive correlation between the vegetative vigour of the plant and the result of the fixation. Vigorous growth gives an increased frequency of cell divisions in the root-tips. There should therefore be a greater number of chromosome plates present to choose from and consequently a better chance of finding really good plates. It may be mentioned here that the difference in the results of fixation noted by the same author, which he thinks may be due to genotypic differences between the plants, was also observed in the material dealt with in this investigation. MÜNTZING's observations refer in the first place to the utility of the plates for accurate determinations of the chromosome numbers. If the observation applies to the morphology of the chromosomes, as is the case in this investigation, the difference between the separate individuals with respect to the higher or lower efficiency value of the plates is much more conspicuous. The disparity, which makes the chromosome plates suitable or unsuitable for morphological analysis, consists essentially in a more or less severe contraction of the chromosomes, which affects the morphologically most important characters, *viz.* the constrictions. »The sharpness of any constriction, and therefore its appearance, must be modified by the degree of contraction» (DARLINGTON, 1932, p. 51).

Of still greater importance than the vigour of the plants is the choice of fixative, for as LEVITSKY (1934, p. 144) says: »The external appearance of chromosomes in fixed and stained preparations is very different according to the kind of fixative employed». The choice must be made in each separate case according to the species of plant and the purpose of the investigation. At the present stage, with respect to technique and methods, one has generally to resort to experiments. Several different kinds of fixatives were therefore tested on the Spitsbergen grasses.

The chrom-acetic formalin fixations specially recommended by Russian cytologists and, indeed, most commonly employed by a number of investigators, did not in any case give satisfactory results for detailed chromosome morphological studies. Without exception they all caused great contraction and swelling. But it should be mentioned that the chromosomes were often beautifully spread in the metaphase plate and therefore counts could very easily be made even in species with very high chromosome numbers. These fixatives have therefore their legitimate use. In the case of serial examinations of chromosome numbers, as for instance in F_2 generations and the like, they are to be

preferred. The chrom-acetic formalin fixatives are cheap to use, staining after such a fixation can often be made without previous bleaching, and in addition the preparations are easily stainable. An excellent advantage, which is of great importance in many cases, is their preservative property, it being possible to keep the material in the fixative for quite a long time. For instance, LANGLET (1932) states that he has preserved material in such a fixative (»Karpechenko») for 5 years without noticing any unfavourable effect, on the contrary, the staining property was even improved. But as mentioned, they are less suitable for chromosome morphological investigations, at any rate in the case of grasses — a fact which is indeed quite evident from the drawings from preparations fixed with these fixatives reproduced by various authors in the literature.

Fixatives such as sublimate formalin, cupric formalin, picric formalin and platin formalin in varying proportions, which are said by LEVITSKY (1934), who first recommended the method, to give exceptionally good results for the purpose of studying the morphology of chromosome, did not by any means give such good slides as might have been expected.

The fixatives which were found to be the best in this connection were those containing osmic acid, and the most satisfactory results for detailed studies were obtained with LA COUR's (1931) 2BD. LA COUR also specially recommends 2BD for grasses, the formula being: 100 cc. 1 p. Ct chromic acid, 100 cc. 1 p. Ct potassium bichromate, 0,1 gr. saponine, 30 cc. 2 p. Ct osmic acid and 30 cc. 5 p. Ct acetic acid.

Besides grasses, 2BD has also given excellent results when used for *Ranunculus* (cf. FLOVIK, 1936), for *Carex* and *Eriophorum* as well as for certain species of *Saxifraga* and *Stellaria.*

For reduction divisions in P.M.C:s I used partly a »Flemming-Newton» modification and partly »Benda» (cf. RANCKEN, 1934). The majority of the fixations were, however, made with a modification of 2BD by adding 15 cc. 2 p. Ct osmic acid to the ordinary solution in accordance with LA COUR's directions. No marked difference could be discovered, however, between the fixing capacity of the above-mentioned fixatives.

The microtome sections varied between 12 and 25 μ in thickness, according to the size of the cells in the respective species, the cells being measured in each separate case. As a rule the thickness of the section was 1—1 $^1/_2$ times the average diameter of the cell. A number of the reduction division slides were prepared by TAYLOR's smear

method (TAYLOR, 1924), and, as was to be expected, these were always most beautiful.

The fixation of reduction divisions was carried out at Tromsö in the spring of 1936, and the following facts are worth mentioning. As far as the majority of high-arctic species are concerned, the reduction divisions took place at night and best between 2 and 5 a. m., at that period of the day when the temperature was lowest, 5—8° C. In the daytime, when the temperature rose to about 15° C. and higher, divisions could not as a rule be observed, and if they occurred they were always very few in number. In Spitsbergen, on the other hand, the divisions in the same species were most frequent in the daytime when the temperature was highest, *i. e.* about 4—8° C., thus corresponding to the night temperature at Tromsö at which the divisions were most frequent. There were exceptions to this rule, *viz. Deschampsia alpina, Poa alpigena* and *Festuca rubra* var. *arenaria.* In these species there was also a high frequency of divisions at the higher temperatures and therefore fixations could be made in the daytime. Several species did not, generally speaking, flower at Tromsö, but in return they attained a more gigantic vegetative development in the higher temperature. Among these species were *Hierochloe alpina, Dupontia Fisheri* and *Festuca ovina* var. *brevifolia.*

The stain employed was gentian violet according to NEWTON's gentian-violet-iodine method (cf. NEWTON and DARLINGTON, 1929) and very satisfactory results were obtained. Staining was difficult in only a very few cases, in which the chromic acid scale recommended by LA COUR (l. c.) had to be employed.

In her study on the morphology of the chromosomes in *Plantaginaceæ*, MCCULLAGH (1934) states that she obtained more satisfactory results with Iron-Alum Hæmatoxylin by HEIDENHAIN's method. This method was also tried in the present investigation, but a comparison of the preparations showed that in no case did Iron-Alum Hæmatoxylin give such well stained, clear and suitable preparations as gentian violet. MCCULLAGH (l. c., p. 3) says that when using gentian violet, »owing to the transparency produced in the chromosomes, comparison of the constrictions was more difficult than when the Hæmatoxylin Iron Alum stain was used». But just this transparency has been found by other workers and also by the present writer to be a great advantage. This property can, however, be entirely eliminated by using deep green filters. Otherwise gentian violet has everything to recommend it. Staining and differentiation are effected very quickly. Thick sections

may be cut and still brilliant stainings obtained, thus avoiding the loss of any material. Besides, as LANGLET (l. c., p. 382) points out: »Ein weiterer Vorteil ist, dass violettes Licht die kürzeste Wellenlänge hat, und demzufolge das Auflösungsvermögen der Objektive maximal wird».

All the reproduced chromosome drawings were made with the aid of an Abbe's camera lucida, employing a Zeiss fluorite objective 100 × and a compensating eyepiece 30 ×. For microphotography, Reichert's Kam V was used, as a rule with the above-mentioned objective and a compensating eyepiece 20 ×. The reproduced magnifications of the drawings and microphotographs are given under the figures in the text and in the explanation of the microphotographs.

As the source of light an illumination arrangement designed by MEURMAN and KARI on BELLING's system was employed.

For measuring chromosomes, different methods have been recommended and employed by different investigators. HEILBORN (1924), who worked with the very small chromosomes in *Carex,* drew the chromosomes in the usual manner with the aid of a camera lucida; the drawings were then placed under a microscope fitted with a low magnifying objective and the measurements were determined by means of an ocular micrometer. GELEI (1921) was the first to use the projection method in its simplest form. This method was later developed and improved by KAGAWA (1927), and was again modified for measuring relatively long chromosome by HASEGAWA (1932). If the chromosomes are lying in their entire length in one and the same optical plane (in the horizontal plane) measurement is most easily performed on a flat camera lucida drawing. In plants having many and relatively long chromosomes it will always be found that a large number of the chromosomes are more or less bent or curved in the vertical plane. In such cases a flat camera lucida drawing cannot be used for purposes of measurement, and the projection methods must then be employed, even if they are open to criticism (cf. NAVASHIN, 1934).

In this investigation HASEGAWA's (l. c.) method was employed. For measuring by this method, which is in principle similar to ordinary survey levelling, a camera lucida was used in connection with the micrometer screw of the microscope. In this way both the horizontal and the vertical distances can be set down graphically and the reconstruction of the actual length of the chromosomes and the position of the constrictions be determined. The method was very efficient in the case of the material investigated here, where the chromosomes have

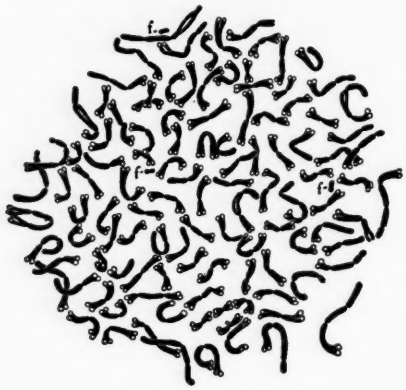
as a rule several well-defined constrictions which could serve, to use HASEGAWA's terminology, as »starting points» and »observing points». With the aid of this method it was possible to analyse entire metaphase plates and idiograms for several species could therefore be drawn up. The use of the method was also considerably facilitated by the finer adjustments of the micrometer screw in the latest types of microscopes.

In the case of the species where a complete chromosome morphological analysis was possible, the recorded average lengths of the various types of chromosomes are based on the measurement of at least 5, as a rule more than 5, metaphase plates, in which specimens of all types present could be identified and measured.

III. DESCRIPTION.

1. ALOPECURUS ALPINUS SM.

Root-tips of three habitually different individuals were fixed. One of these individuals differed conspicuously from the other material by means of its robust appearance. The plant can best be characterized as a gigas type — tall with broad leaves, thick straws, large spikelets, etc. The number of chromosomes in this individual could not be determined exactly in root-tip preparations, but it was ascertained that the number was above 120. In the other two individuals lower, but differing chromosome numbers were found, *viz.* 2n = 112 + 3ff and 114 + 2ff.



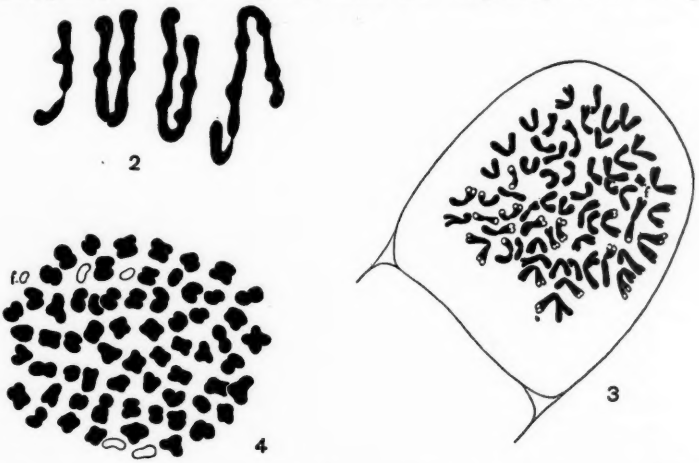
1

Fig. 1. Somatic metaphase plate of *Alopecurus alpinus*, from a plant with 2n = 112 + 3ff. — Magnification: 2700 ×.

It may be mentioned here that AVDULOV (1931) gives the number 2n = 70 for the *Alopecurus alpinus* var. *elatus* examined by him, and MÜNTZING (1936) records the very high number 2n = > 100 for *Alopecurus antarcticus*.

Fig. 1 shows a somatic metaphase plate from the double octoploid plant having the number 2n = 112 + 3ff. The fragment chromosomes

marked »f», can be clearly seen to have a median constriction. These fragments are all of the same size and measure on an average 0,7 μ in length, whereas the shortest normal chromosome measures 3,0 μ and the longest 5,8 μ. The chromosomes in *Alopecurus alpinus* are therefore considerably shorter than those in *A. pratensis* with the lower number $2n = 28$, in which RANCKEN (1934) found that the majority of the chromosomes are from 6 to 7 μ in length. In *Alopecurus* the size of the chromosomes thus seems to diminish with an increasing degree of polyploidy. As in *A. alpinus*, there also frequently occur a varying



Figs. 2—4. Meiosis in *Alopecurus alpinus*. — Fig. 2, multivalents in side view (1III + 1IV + 1V + 1 VI) drawn from different P.M.C:s. — Fig. 3, polar view of a metaphase II plate of the plant with $2n = 112 + 3ff$, in which, owing to irregular numerical segregation, 59 + 1f chromosomes can be counted. — Fig. 4, polar view of a metaphase I plate from another plant showing 68 units, 5 of which are univalents (the white ones). One of the univalents (f) is probably a fragment. — Magnification: 2700 ×.

number of chromosome fragments in *A. pratensis*, but the fragments in the letter species are, according to RANCKEN (l. c.), very large, their length being nearly half that of the normal chromosomes. In *A. alpinus* the length of the fragments is only one-fourth of that of the shortest normal chromosomes and the fragments in this species may therefore be said to be of quite a different type.

A detailed morphological analysis of the chromosomes is obviously impossible owing to the high chromosome number and also because the majority of the chromosomes are bent to an unusual degree with

the ends straight out from the plate towards the poles. From Fig. 1 it will be seen, however, that several chromosomes, especially those of the longest types, have in addition to the primary constriction also one or more secondary constrictions, in the same manner as RANCKEN found in *A. pratensis*.

Observations of the reduction divisions, which as regards this species as well as other species dealt with here are limited to the P.M.C:s, show that very great aberrations of various kinds occur. Such things as univalents outside the metaphase plates, lagging chromosomes at anaphase I and II, etc. are very common.

Although metaphase plates of the first division in polar view appear mostly to consist of ordinary bivalents, in side view multivalent groups of conjugated chromosomes can very frequently be seen. Trivalents, quadrivalents, quinquevalents and sexivalents could be observed. Drawings of such multivalent chains are shown in Fig. 2. Judging from the length of isolated chains, it is more than likely that conjugated groups of still higher orders occur. But it should be pointed out that owing to the high chromosome numbers present in this species it is generally very difficult to determine for certain whether there is a real connection between pairs lying close together or whether they are simply lying in close proximity.

It is highly probable that the presence of numerous homologous chromosomes capable of conjugating and forming irregular first division groups along with the simultaneous occurrence of univalents, lead to an unequal numerical distribution to the daughter nuclei. Chromosome counts at metaphase II also showed, as was to be expected, that such an irregular numerical segregation is common. Fig. 3 from a plant, the somatic chromosome number of which was found to be 112 + 3ff, thus shows a metaphase II with the chromosome number 59 + 1f instead of the number 56 + ff, as would be the case in normal segregation.

Fig. 4 shows a metaphase I from the gigas type mentioned above. Altogether 68 units can be counted in this metaphase plate, 5 of which are univalents. One of these univalents, marked »f», must on account of its small size be regarded as a fragment. If the other units are looked upon as bivalents, the chromosome number in this individual will be 130 + 1f. It is probable, however, that some of these units are multivalents and therefore the chromosome number is still higher than that indicated by the reproduced metaphase plate in Fig. 4.

At anaphase and telophase of both the first and the second division a varying number of chromosomes and fragments, excluded from the

great mass, could be seen lying in the spindle between the poles or scattered round in the plasm, as shown in Fig. 5 of a late anaphase II. Quite a number of such chromosomes will certainly not be included in the newly formed daughter nuclei but will produce their own nuclei or they will be absorbed in the plasm. The latter is in all probability the most common occurrence, for micronuclei were comparatively seldom observed at interkinesis and the formation of tetrads took place quite normally. It seems to be mostly small chromosomes and fragments which are eliminated in this manner.

In view of the irregularities seen to occur at meiosis it is quite natural that different chromosome numbers are found in different individuals of this species. As the numbers vary between very wide limits we have a satisfactory explanation of the great variability prevalent in the species. As MEURMAN (1929 b) points out, with regard to the analogous case in *Prunus laurocerasus,* it is evident that no constant chromosome number exists. The number $2n = 112 + 3ff$ found in one individual, which may be said to form an even multiple of 7 — the basic number in *Alopecurus* — can surely be regarded as quite as accidental as the other numbers found, $2n = 114 + 2ff$ and approximately $130 + 1f$. Similar aneuploid chromosome numbers in polyploid species have been recorded by several other workers; here reference will only be made to DARLINGTON's tabulation of these species (DARLINGTON, 1936, p. 220).

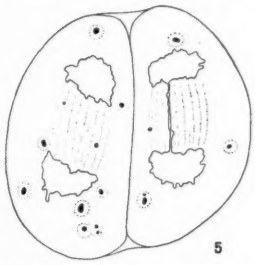
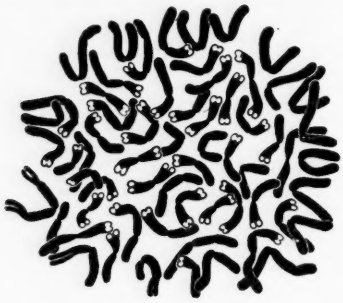


Fig. 5. Meiosis in *Alopecurus alpinus.* Side view of a late anaphase II where several chromosomes and fragments can be seen scattered around in the plasm. — Magnification: 1350 ×.

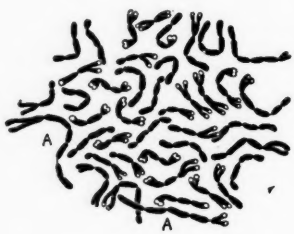
The circumstance that gametes with greatly varying chromosome numbers are capable of fertilisation and that the new individuals look quite normal in spite of a considerable loss or addition of chromosomes is quite interesting. MEURMAN (l. c.) explains this condition by saying that the high polyploid gametes are probably viable independent of their actual chromosome number. The fundamental chromosome types are represented so many times that a loss or addition of single chromosomes has no longer any serious effect, and therefore the aberrant numbers are not eliminated.

2. ARCTAGROSTIS LATIFOLIA (R. BR.) GRISEB.

The examined individuals, originating from three different localities in Coles Bay, were found to have the chromosome number $2n = 62$, as appears from the somatic metaphase plate in Fig. 6. This number is not a multiple of any basic number previously known in the *Gramineæ* family. Its evident constant occurrence within an extensive area (Coles Bay) can only be explained on the assumption of an exclusively vegetative propagation. This species flowers also very late and it seems quite out of the question for seed to ripen in Spitsbergen. Investigations of material from other localities and of the reduction divisions must be made before any conclusions can be drawn with regard to the origin



6



7

Figs. 6 and 7. Somatic metaphase plates. — Fig. 6, *Arctagrostis latifolia*, $2n = 62$; fixed in Navashin's fluid, the chromosomes being swollen and only the primary constrictions clearly marked. — Fig. 7, *Arctophila fulva*, $2n = 42$; only two long chromosomes of the *A* type being present. — Magnification: 2700 ×.

and the constancy of the chromosome numbers found. The question must, however, remain open for the present, as material for more extensive studies was not available.

From Fig. 6 it will appear that there is a conspicuous difference between the chromosomes in the species under discussion and those in the other species of grass dealt with in the present paper. The difference, however, is due essentially to the fixative employed, in this case »Navashin» — that is, a chrom-acetic acid formalin fixation. The chromosomes are greatly compressed along their longitudinal axis and therefore appear to be swollen. The primary constriction is clearly defined, however, in all chromosomes, while secondary constrictions can be observed only in a few.

When LA COUR's 2BD was used as fixative, the chromosomes in

Arctagrostis latifolia acquired a much more delicate appearance. They were slender, but were considerably longer than those in the other species in question here, and it may be pointed out that secondary constrictions were present in relatively large numbers in the majority of the chromosomes, and that these constrictions, especially in the longest chromosomes, proved themselves to belong to the category of »long» constrictions. But owing to the fact that the chromosomes were relatively long and had a tendency of twining round one another, together with the simultaneous appearance of long constrictions, counts could not possibly be made in the preparations fixed with 2BD. Therefore the chrom-acetic acid formalin fixations have their indisputable justification; but, as already mentioned on p. 270, they proved to be unsuitable for morphological studies of the chromosomes, at least that was the case in all the grasses investigated by the present writer.

A point worth mentioning in this connection is that the contraction caused by the fixative appears in the first place to involve the secondary constrictions. The primary constrictions (cf. Fig. 6) are nearly always clearly defined, whereas the secondary constrictions disappear entirely. This may be explained by the fact that the centromere, which is distinguished by the primary constriction, does not react in the same manner to the different fixatives as the chromatin.

3. ARCTOPHILA FULVA (TRIN.) RUPR.

This species is a hexaploid with the chromosome number $2n = 42$. From Fig. 7 it will be seen that the chromosomes are rather highly segmented, a large number of secondary constrictions being present. The length of the chromosomes varies considerably. The longest specimens measure about 7,5 μ and the shortest only 2,5 μ. Chromosomes of the type marked *A* could easily be distinguished from the others in that they are nearly 2 μ longer than the chromosomes next in size, and this type is represented twice. In Fig. 7 these two chromosomes are seen in the periphery of the plate, at 6 o'clock and at 8 o'clock. The fact that there are only two specimens of a type thus furnishes definite evidence that *A. fulva* is of allopolyploid origin.

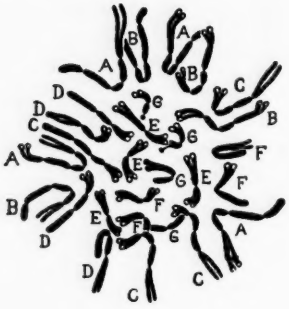
As in the case of the preceding species, no material for studying meiosis could be obtained.

4. CALAMAGROSTIS NEGLECTA (EHRH.) P. B.

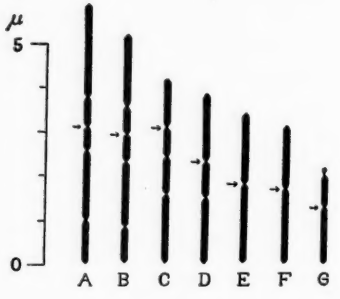
The chromosome number is $2n = 28$. A characteristic metaphase plate with this number is reproduced in Fig. 8. AVDULOV (1931) gives the number $2n = 68—72$ for the *C. neglecta* examined by him — thus

obviously a decaploid form. The low number, $2n = 28$, in the high arctic form investigated here is noteworthy, for we should sooner expect to find the highest number.

It may be mentioned that the fixation was exceedingly successful. As a rule the chromosomes lay very beautifully scattered and the constrictions were sharply defined, which to a great extent facilitated a complete chromosome morphological analysis. The different types of chromosomes are marked here with capital letters in alphabetical order, *A* denoting the longest type and *G* the shortest. The same basis of



8



9

Figs. 8 and 9. *Calamagrostis neglecta*, $2n = 28$. — Fig. 8, somatic metaphase plate where all the chromosome types can be seen represented four times, but there are only two satellite-bearing chromosomes of the *G* type. — Magnification: 3600 ×. — Fig. 9, diagrammatic representation of the chromosome types present in the somatic complement. The primary constrictions are marked by arrows. The *A* and *B* types, together with *E* and *F* are strikingly alike in all respects with the exception of the total length.

classification, *viz.* the length of the chromosomes, is also employed in the case of the other species dealt with in this work, where the chromosome complement was subjected to a morphological analysis.

Fig. 8 shows the characteristic shape of the majority of the chromosome types and their morphological features otherwise. The average figures obtained in the measurements made are given in Table 1, and the diagram of the types in Fig. 9 is constructed on the basis of this table.

In connection with these figures a few remarks may be made. There seems to be a certain difference between two and two examples of the *A* and *C* types of chromosomes. In Fig. 8 the two longest *A* type of chromosomes are seen at 5 o'clock and 11 o'clock, and the

other two, somewhat shorter, at 1 o'clock and 9 o'clock. This difference in length discernible in Fig. 8 could not, however, be observed for certain in all otherwise good metaphase plates. Further, the *G* type of chromosome must be mentioned especially. In the chromosome complement of the individuals examined there always occurred two specimens of this type with satellites and two specimens without. Otherwise the length of the chromosomes and the position of the primary constriction are exactly the same in both cases. Each of the other types

TABLE 1. *The average length of the different chromosome types in Calamagrostis neglecta.*

Type	*A*	*B*	*C*	*D*	*E*	*F*	*G*
Length of the segments in μ	2,1	1,7					
	0,7	0,7	1,1				
	0,5	0,6	0,7	1,5			(0,1)
	1,6	1,5	0,8	0,8	1,6	1,4	0,7
	1,0	0,7	1,6	1,5	1,8	1,7	1,3
Total length in μ	5,9	5,2	4,2	3,8	3,4	3,1	2,1

are represented by four morphologically homologous chromosomes. If the morphological characteristics of chromosomes are made the basis of the terms autopolyploidy and allopolyploidy, it may be said that here we have a borderline case. Probably it is a question of a cross between different forms which differ from one another in a chromosome morphological respect, one having satellite-bearing and the other non-satellite-bearing *G* type chromosomes.

A somewhat rougher classification of the chromosomes in *C. neglecta* into different types, where the small differences in length would not be considered of decisive importance, but where the number and the type of the constrictions and their relative positions are made the foundation, would result in a division of all the chromosomes present into 5 types instead of 7. A close examination of the diagram of types (Fig. 9) will illustrate this. The *A* and *B* types resemble each other very closely as regards segmentation, the relative lengths of the different segments and the position of the primary constriction. Fig. 8 also shows the similarity in shape — both are V-shaped. On the whole they are very difficult to distinguish from each other under the microscope without making a careful measurement of the individual segments. The differ-

ence in length between the two types has reference to the distal segments, which are somewhat longer in the *A* type than in the *B* type. The corresponding intercalary segments in both types are, generally speaking, of the same length (cf. Table 1 and Fig. 9). — Further, it appears from the diagram of types (Fig. 9) that the *E* and *F* types of chromosomes are strikingly alike. Chromosomes of these types have a submedian constriction — the primary. On account of the similar position of this constriction in both types, they have exactly the same shape, again the V-shape. The only possible distinguishing feature is the total length, but even this difference in length is very small, about 0,3 μ, and is within the limits of the expected error of measurement.

During the reduction divisions there appear along with bivalents frequently other configurations. Univalents, bivalents and quadrivalents can be frequently observed, but in limited numbers in each cell. In side view the bivalents are mostly in the form of a compact ring; cross-shaped bivalents and other side-view figures are less frequent. Fig. 10, from a metaphase I in side view, shows $11_{II} + 2_{I} + 1_{IV}$. Fig. 11 shows $10_{II} + 1_{I} + 1_{III} + 1_{IV}$; the quadrivalent occurring here is of a somewhat curious shape — compare the microphotograph in Plate I, Fig. 4. Further, the univalent and the trivalent reproduced in Fig. 11 can be plainly seen in Plate I, Fig. 6. Figs. 12 and 13 of metaphase I plates in polar view show $12_{II} + 1_{IV}$ and $13_{II} + 2_{I}$ respectively.

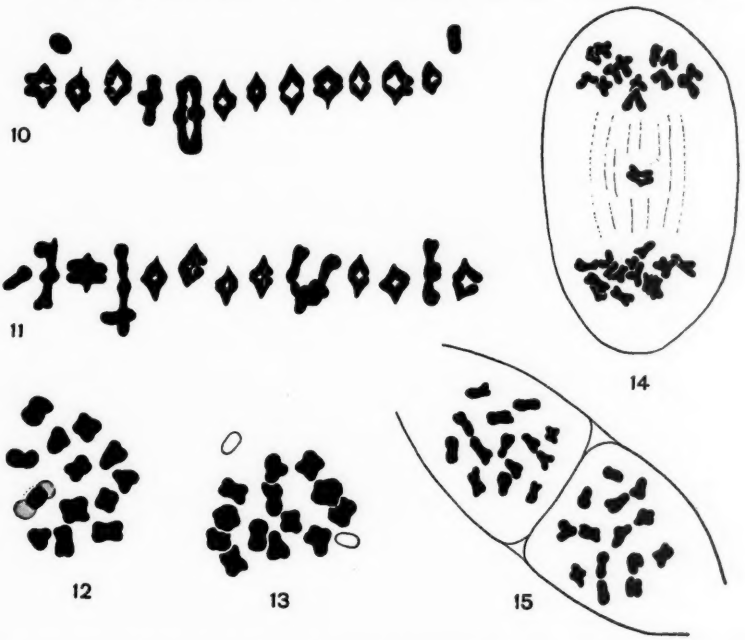
The lowest number of bivalents observed in one cell was 10, and not more than one quadrivalent was ever seen in any cell. A complete analysis of metaphase I in 31 cells gave the following result:

Configurations	Number of cells	Configurations	Number of cells
14_{II}	13	$10_{II} + 1_{I} + 1_{III} + 1_{IV}$	1
$12_{II} + 1_{IV}$	10	$13_{II} + 2_{I}$	1
$11_{II} + 2_{I} + 1_{IV}$	3	$12_{II} + 4_{I}$	1
$12_{II} + 1_{I} + 1_{III}$	2		

In agreement with these irregularities a more unequal numerical distribution of the chromosomes should be expected. But although it may be taken for granted that such an unequal distribution occurs sometimes, no certain case was met with. Fig. 14 shows an anaphase I with 13 chromosomes at one pole and 14 at the other, and one lagging univalent on the point of dividing is situated in the middle of the spindle between the two poles. It is improbable that this chromosome will reach either of the poles in time to be included in one of the new

daughter nuclei, it will instead either be absorbed in the plasm or form its own nucleus. If it reaches one of the poles, it will, from its position in the spindle, pass to the pole having already 14 chromosomes. A number of metaphase II plates were counted, but all of them contained 14 chromosomes each, as appears from Fig. 15 and Plate I, Fig. 10.

Secondary associations were sometimes observed at both metaphase



Figs. 10—15. Meiosis in *Calamagrostis neglecta*. — Figs. 10 and 11, side views of metaphase I plates, separately drawn, showing $11_{II} + 2_I + 1_{IV}$ and $10_{II} + 1_I + 1_{III} + 1_{IV}$ respectively. — Figs. 12 and 13, polar views of metaphase I plates showing $12_{II} + 1_{IV}$ and $13_{II} + 2_I$ respectively. — Fig. 14, side view of anaphase I, distribution 13—1—14; the lagging univalent is split. — Fig. 15, polar view of a metaphase II, 14 chromosomes can be counted in each plate. — Magnification: 2700 ×.

I and II. Then there most frequently occurred 4 groups of secondary associations, each group comprising two bivalents so that really only 10 separate units could be counted at metaphase I (cf. Plate I, Fig. 9). A similar tendency to form secondary associations at metaphase II will be seen in Plate I, Fig. 10.

Further, it may be mentioned that the pollen formation in *C. neglecta* was quite normal, in contradistinction to the species *C. obtusata*,

C. purpurea and *C. lapponica*, in which STENAR (1932) found that most of the pollen grains were incapable of germination, and that at least *C. obtusata* and *C. purpurea* are probably apomictic.

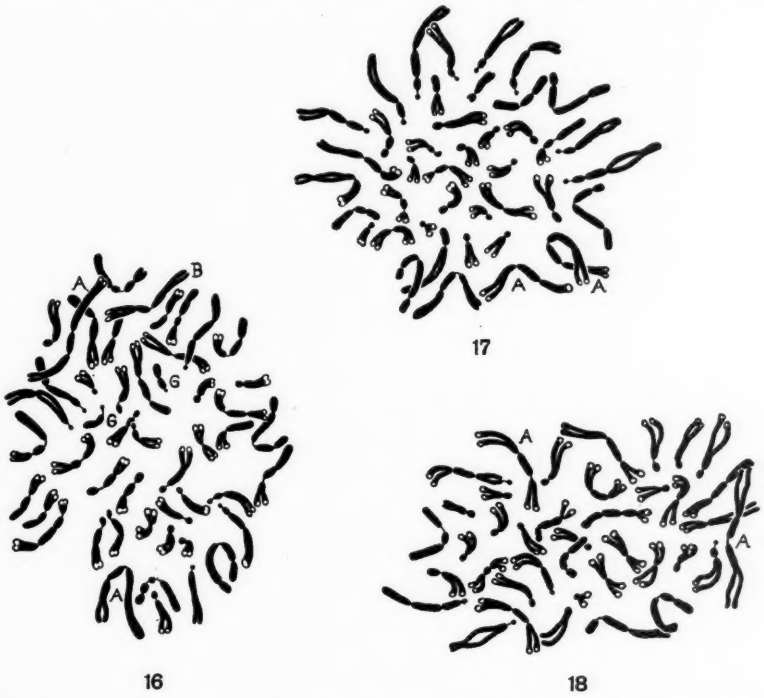
5. DESCHAMPSIA ALPINA ROEM. ET SCHULT.

Of this typically viviparous and highly polymorphous species, three morphologically very different biotypes were selected for close investigation. One biotype characteristic of the species, which had a comparatively robust appearance and was highly viviparous with well developed bulbils, proved itself to be a heptaploid with the chromosome number $2n = 49$ (Fig. 16). — Another biotype, which as far as external morphological properties are concerned, seemed to have much in common with *D. cæspitosa* f. *arctica* (TRIN.), had the number $2n = 41$ (Fig. 17). This type was considerably smaller than the above-mentioned 49-chromosome type, and the spikelets were less distinctly viviparous. — The third biotype examined was in every respect dwarfy with thin and short straws, narrow leaves, narrow apex with slender apical branches and small spikelets. Even in this type an aneuploid chromosome number was found, *viz.* $2n = 39$ (Fig. 18). In this case the vivipary was very slight; only a few bulbils could be seen without the aid of a magnifying glass and in many spikelets the otherwise usual metamorphosis of the glumella was hardly visible.

The differences found in the chromosome numbers are of interest in so far as they furnish a satisfactory explanation of the pronounced polymorphy in *D. alpina*. What is of more interest in connection with the problem of vivipary and with the various views held concerning that problem is the morphology of the chromosomes. Of the above-mentioned three biotypes, the best preparations were obtained from the 49-chromosome biotype, which was otherwise subjected to a special examination owing to the fact that the chromosome number in this type is a multiple of 7 — the basic number in the genus *Deschampsia* — and may thus be assumed to possess all the chromosome types characteristic of the species.

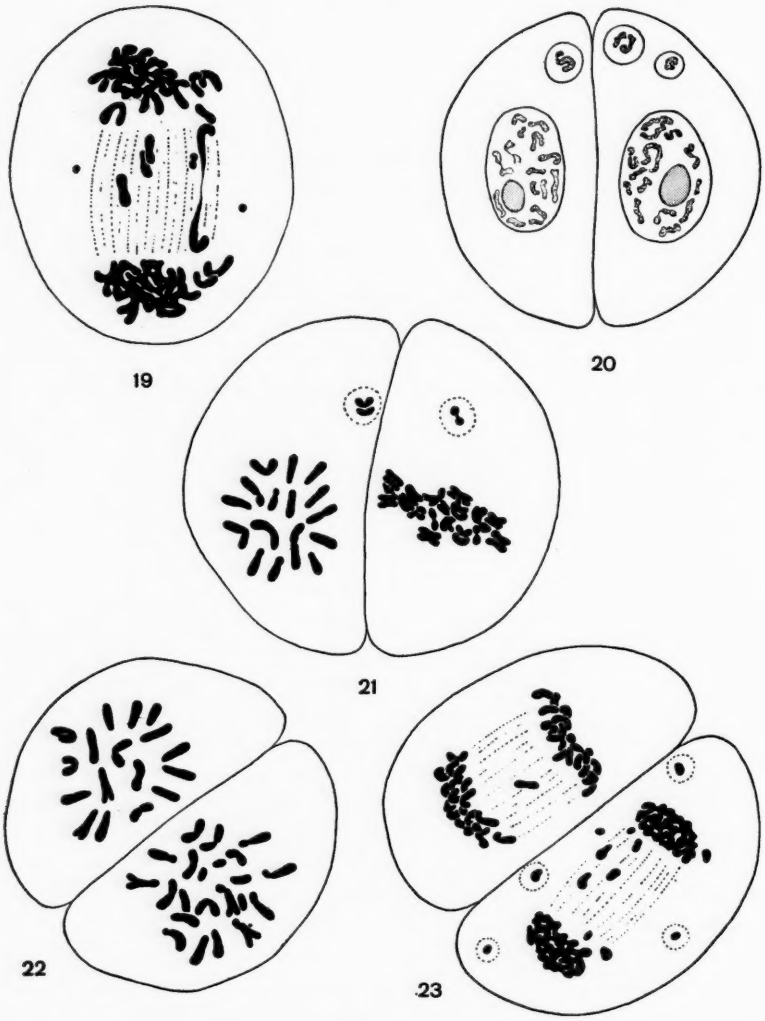
In the metaphase plate reproduced in Fig. 16 will be seen the chromosome morphological details which could be established for certain. No complete analysis of the entire chromosome complement was possible in the available material, but there are chromosomes which are so conspicuously characteristic and so widely different from the bulk of chromosomes that they cannot escape discovery even in a cursory glance in the microscope. This is true in particular of chromo-

somes of the *A* and *G* types (cf. Fig. 16). The *A* type chromosomes are considerably longer than the others; they have a submedian primary constriction and are as a rule V-shaped. An always prominent secondary constriction is found in the shorter arm, close to its proximal end. The intercalary segment, thus resulting, measures on the average



Figs. 16—18. Somatic metaphase plates from different biotypes of *Deschampsia alpina*. — Fig. 16, from a biotype with $2n = 49$; only two long chromosomes of the *A* type and two of the short, satellite-bearing chromosomes of the *G* type are to be found. — Figs. 17 and 18, from biotypes with the chromosome numbers $2n = 41$ and $2n = 39$ respectively. In both the plates only two *A* type chromosomes can be identified. — Magnification: 3600 ×.

0,9 μ — the total length of the type amounts to 5,8 μ. Chromosomes of this type were always found to be represented twice. In Fig. 16, one of these chromosomes, which possesses the characteristic V-shape of the type, will be found at 6 o'clock, and the other, which in this case is more straight, will be seen at 11 o'clock — both chromosomes are situated in the periphery of the plate. Another type designated *B*,



Figs. 19—23. Meiosis in *Deschampsia alpina* (Figs. 19—22 from the 39-chromosome and Fig. 23 from the 41-chromosome biotype). — Fig. 19, side view of anaphase I showing lagging chromosomes and two fragments. — Fig. 20, interkinesis with micronuclei. — Fig. 21, metaphase II; the plate in polar view shows 16 chromosomes. The micronuclei form their own spindles. — Fig. 22, metaphase II with both the plates in polar view; in one 17 and in the other 22 chromosomes can be counted. — Fig. 23, side view of anaphase II, showing lagging chromosomes in the spindle, also chromosomes scattered around in the plasm on the point of forming micronuclei. — Magnification: 2700 ×.

which very closely resembles the *A* type as regards segmentation and shape, is seen in the same figure, at 12 o'clock; but chromosomes of this type are as much as 1,4 μ shorter — total length 4,4 μ — and therefore the two types can hardly be mistaken for one another. The number of the *B* type chromosomes could not be determined for certain in any of the plates examined, but they seem to be represented at most three times.

Special mention must also be made of the chromosomes designated *G*, which are just as easy to identify as the *A* type. Besides being the shortest (approximately 1,2 μ), they are also characterized by being satellite-bearing. These chromosomes, too, are present to the number of two. In Fig. 16 these two chromosomes can be seen nearer the centre of the plate.

As regards the other chromosomes, a few types are easily distinguishable, but the correct number of chromosomes belonging to each type cannot be given with certainty; still it may be said that none of the more characteristic types are represented 7 times, *i. e.* to a number corresponding to that of the chromosome sets. Several chromosomes have satellites or have a very short proximal segment, which is separated from the other portion at the primary constriction.

The above chromosome morphological data indicate quite plainly the existence of allopolyploidy, a fact which is also supported to a certain extent by the chromosome number ($2n = 49$).

The metaphase drawings from the 41- and 39-chromosome biotypes respectively reproduced in Figs. 17 and 18 make no pretence to being correct in all chromosome morphological details. They have been included here more to show the number of chromosomes. But even in these two biotypes the two chromosomes of the *A* type could be clearly identified and, like the 49-chromosome biotype, they must therefore be regarded as being of allopolyploid origin. In Fig. 17 these two chromosomes are seen alongside each other at 5 o'clock, and in Fig. 18 one of them, at 3 o'clock, can be seen quite plainly. The equally characteristic *G* type of chromosomes were looked for but could not be discovered, whence it must be assumed that they are altogether missing in these biotypes with lower chromosome numbers.

The behaviour of the chromosomes during the reduction divisions is on the whole the same in all three biotypes mentioned above, and they will therefore be described collectively. Both first and second divisions run a highly abnormal course. Metaphase I regularly showed a large number of univalents lying outside the plate. At anaphase I there

frequently occur lagging chromosomes, mostly univalents, as shown in Fig. 19 from the 30-chromosome biotype, and a number of these lagging chromosomes do not reach the poles in time to be included in the new daughter nuclei, but form micronuclei instead, as appears from Fig. 20 from the 39-chromosome biotype. Occasionally these micronuclei are found situated very close to the normal nuclei and at metaphase II they will probably be included in the latter. But frequently they lie far from the normal nuclei and then they act more independently in that they form their own metaphase II plates, as shown in Fig. 21 and Plate I, Fig. 7. An irregular numerical distribution must necessarily occur in all cases on account of the aneuploid chromosome numbers. In the 39-chromosome biotype a number of metaphase II plates could be counted. The most extreme instance of irregular distribution found was the segregation of 13 : 26. In Fig. 21 from a metaphase II 16 chromosomes are seen in one of the plates. In this case the segregation must have been 16 : 2 : 21. In Fig. 22 both plates can be seen in polar view and the segregation here is 17 : 22.

Frequently several very small lagging chromosomes could be seen in the spindle or scattered about in the plasm at anaphase I. These chromosomes are evidently the result of fragmentation. In Fig. 19 two such fragments are seen lying between the poles.

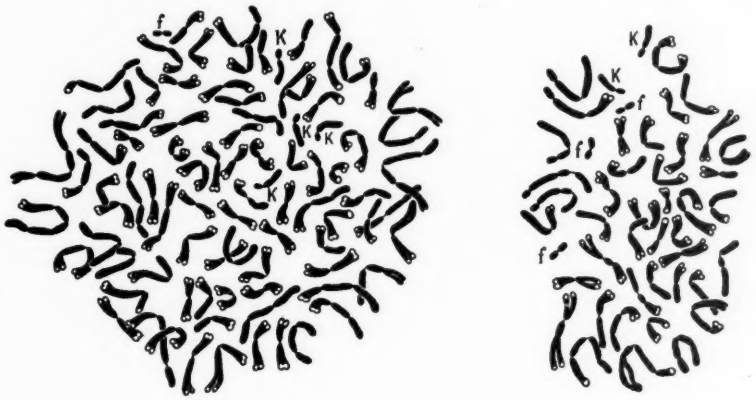
Anaphase II exhibited the same irregular conditions as anaphase I. Lagging chromosomes occurred in varying numbers. Fig. 23 from the 41-chromosome biotype shows a fairly typical instance. The lagging chromosomes here also frequently constitute micronuclei. In the tetrad stage dyads, triads, pentads, etc. could be observed. A great part of the pollen produced seemed to be morphologically good, in the 39-chromosome biotype about 60 per cent, but as was to be expected from the irregularities occurring at meiosis the size of the pollen was extremely variable.

6. DUPONTIA FISHERI R. BR.

Dupontia occurs in two habitually very different forms, which are, however, linked by intermediates (cf. SCHOLANDER, 1934). The main form, *D. Fisheri* R. BR., is more robust in its vegetative and floral parts, but is on the whole somewhat lower than the other form, *D. psilosantha* RUPR. Though certain morphological differences occur, it may be said that these differences are mainly quantitative. According to SCHOLANDER's opinion, there are hardly any grounds for separating these forms into two different species, but, in his opinion, RUPRECHT's

form well deserves the rank of a variety and is suggested by the said author as: *Dupontia Fisheri* R. Br. var. *psilosantha* (Rupr.) Scholander.

There seems to exist a certain difference in geographical distribution between these two forms (cf. Scholander, l. c.). In Greenland the main form seems to be very rare; in Nova Zembla the var. *psilosantha* is very rare and in South Spitsbergen the latter is about as common as the main form. In Northern Spitsbergen, however, only the main form was seen by Scholander. The main form thus seems



24 25

Figs. 24 and 25. Somatic metaphase plates of *Dupontia*. — Fig. 24, *D. Fisheri*, $2n = 88 + 1f$; four *K* type chromosomes can be identified. — Fig. 25, *D. Fisheri* v. *psilosantha*, $2n = 44 + 3ff$; only two *K* type chromosomes are to be found. — Magnification: 3600 ×.

to be best suited for the climatically unfavourable regions where var. *psilosantha* is missing or is but very sparsely represented.

In view of the above-mentioned facts, the cytological data are of considerable interest. The main form, *D. Fisheri*, was found to have the chromosome number $2n = 88$ in addition to a varying number of fragments. Fig. 24 shows a metaphase plate from an individual with the number $2n = 88 + 1f$. Another individual was found to have the number $2n = 88 + 3ff$. Owing to the large number of chromosomes present in this species chromosome morphological studies were attended with difficulties. One of the types present in this chromosome complement could nevertheless be distinguished from the others, as it differed widely in appearance. Besides being the shortest, chromosomes

of this type, marked *K* in Fig. 24, are distinguished by the fact that the primary constriction has a more terminal position than in any of the other chromosomes. The highest number of these *K* type chromosomes observed was four, and in Fig. 24 all four of them can be plainly seen.

The above-mentioned fragments were all of exactly the same size and appearance. They possess a well-defined median constriction (cf. Fig. 24).

In view of the chromosome number ($2n = 88$) the basic number must be assumed to be 11. *D. Fisheri* is therefore to be regarded as an octoploid and the presence of only 4 chromosomes of the *K* type may thus be taken as evidence of its being an allopolyploid.

7. DUPONTIA FISHERI R. BR. VAR. PSILOSANTHA (RUPR.) SCHOL.

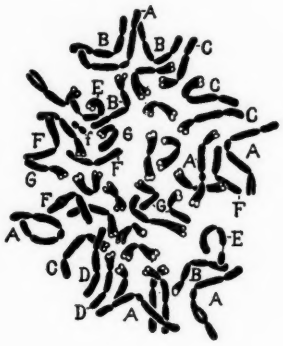
The chromosome number of this form is $2n = 44 + ff$. Fig. 25 shows a metaphase plate from an individual with the number $2n = 44 + 3ff$. In this case, too, the chromosome number is a multiple of 11. Apart from the fragments, the number of chromosomes in var. *psilosantha* is exactly half the number found in the main form, *D. Fisheri*. A particularly interesting feature is that in var. *psilosantha* there are also chromosomes which are morphologically homologous with the *K* type chromosomes found in *D. Fisheri*, and these chromosomes are represented twice, while in *D. Fisheri* they are represented four times. In Fig. 25 these two chromosomes of the *K* type can be seen at 12 o'clock in the periphery of the plate. It should be mentioned that the fragments occurring are morphologically exactly alike in both forms. It was not possible to decide in this investigation whether these fragments were also identical in both cases, but the fact that they are morphologically homologous furnishes a certain ground for assuming that they have a common origin.

The chromosome numbers present, $2n = 44$ and 88, and the occurrence of two chromosomes of the *K* type in the 44-chromosome form and four in the 88-chromosome form constitute good reasons for assuming that the 88-chromosome *D. Fisheri* is derived from the 44-chromosome var. *psilosantha* by a simple chromosome doubling. The var. *psilosantha* must of course be regarded as the primary form, from which the so-called main form, *D. Fisheri* has arisen. *D. Fisheri* furnishes another example of the fact that purely quantitative changes in chromosome number are of considerable evolutionary importance. As already mentioned, the most obvious external morphological differences between the two forms are essentially quantitative. Evidently

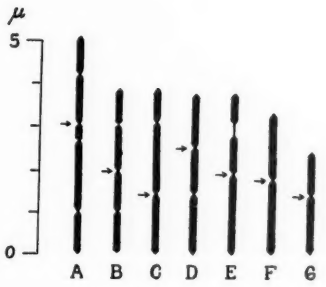
there is a certain difference in the geographical distribution of the two forms. But whether there is also, as may be expected in a case of this kind (cf. MÜNTZING, 1936), any other ecological difference cannot be determined from the evidence avaliable.

8. FESTUCA RUBRA L. VAR. ARENARIA (OSB.) E. FRIES.

The somatic chromosome number in *F. rubra* has already been given by several authors (cf. TISCHLER, 1931, 1936). The numbers 2n = 14, 42, 56 and 70 have been found. For the var. *arenaria*,



26



27

Figs. 26 and 27. *Festuca rubra* v. *arenaria*. — Fig. 26, somatic metaphase plate of a plant with 2n = 42 + 1f; the characteristic *A* type chromosomes can be identified to the number of six. — Magnification: 3600 ×. — Fig. 27, diagrammatic representation of the chromosome types present in the somatic complement. The primary constrictions are marked by arrows.

NAKAJIMA (1930) gives the number 2n = 42, and this number was also found in the var. *arenaria* from Spitsbergen. One individual was found to have the number 2n = 42 + 1f (Fig. 26). The morphology of the chromosomes was subjected to a close study. The results of these investigations are shown in Table 2 and in the diagram of types, Fig. 27. Altogether 7 types of chromosomes can be distinguished, each type being represented 6 times. The chromosomes in *Festuca* appear generally to have a certain tendency to be bent with the ends pointing out from the plate towards the poles. A great many of the chromosomes were also most frequently split, thus all of them do not reach complete metaphase at the same time. This circumstance, together with

the relatively high chromosome number, made an accurate analysis difficult. Thus it was not possible in any single plate to classify all the 42 chromosomes, but in some plates the maximal number of chromosomes of a particular type could be fixed at 6 and in other plates the same number of another type, and so on. The most easily identifiable types are *A*, *E* and *G*. Of these, the *A* and *E* types are of special interest. The average total length of the *A* type chromosomes is 5,1 μ, but the next in length, the *B* type, measures 3,8 μ.

TABLE 2. *The average length of the different chromosome types in Festuca rubra var. arenaria.*

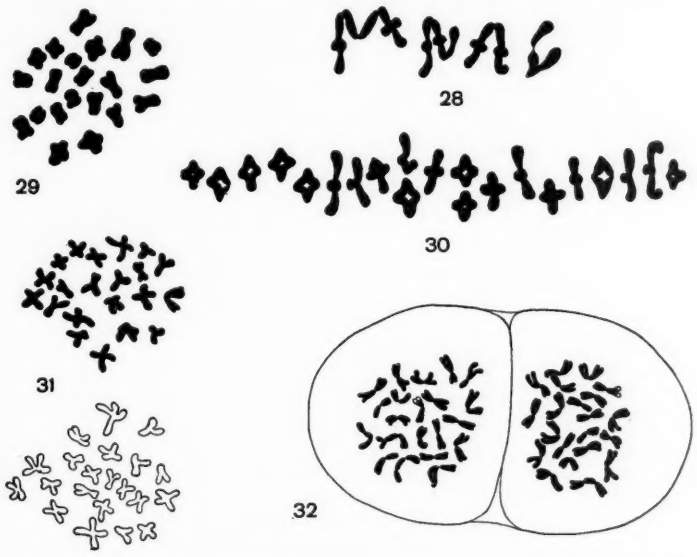
Type	*A*	*B*	*C*	*D*	*E*	*F*	*G*
Length of the segments in μ	0,9						
	1,2	0,7					
	0,3	1,1	0,7	1,2	0,7		
	1,7	1,0	1,7	1,1	0,9	1,5	1,0
	1,0	1,0	1,4	1,4	1,9	1,8	1,4
Total length in μ	5,1	3,8	3,8	3,7	3,5	3,3	2,4

This difference in length is so great that on measurement the *A* type chromosomes cannot be mistaken for chromosomes belonging to other types. Besides being the longest, chromosomes of the *A* type consist of more segments than the others; an important distinguishing feature is furnished by the short, about 0,3 μ, intercalary segment. In Fig. 26 the 6 specimens of these chromosomes are plainly visible. The most characteristic feature of the *E* type of chromosomes is that they often appear with a long secondary constriction (cf. Figs. 26 and 27). Long constrictions were never observed in the other chromosome types.

During the reduction divisions various kinds of irregularities occur, but they are not very frequent. Univalents, trivalents, quadrivalents and sexivalents were met with in addition to the ordinary bivalents in about 6 per cent of the cells examined. Multivalents, drawn from various cells, are shown in Fig. 28. In Figs. 29 and 30, in polar and side view respectively, will be seen the most regular occurrence with 21 bivalents. On the whole anaphase I runs a normal course with a segregation of 21—21 (Fig. 31). Lagging chromosomes could be observed in only a few cases. The same regular distribution (21—21)

was invariably found at metaphase II (Fig. 32). Thus an unequal numerical distribution of the chromosomes seems to be an exceptional occurrence despite the non-disjunctional configurations occurring at metaphase I. A rare case of lagging at anaphase II will be seen in Plate I, Fig. 8.

As appears from the above conditions, meiosis does not therefore



Figs. 28—32. Meiosis in *Festuca rubra* v. *arenaria*. — Fig. 28, multivalents in side view ($1_{VI} + 1_V + 1_{IV} + 1_{III}$) drawn from different P.M.C:s. — Fig. 29, polar view of metaphase I with 21 bivalents. — Fig. 30, side view of metaphase I with 21 bivalents separately drawn. — Fig. 31, polar view of anaphase I, both plates separately drawn, showing the normal segregation (21—21). — Fig. 32, metaphase II with both plates in polar view, 21 chromosomes can be counted in each plate. — Magnification: 2700 ×.

present any typical indication of autopolyploidy. Still, the occurrence, although infrequent, of sexivalents and other multivalent groups, together with the result of the chromosome morphological studies, point to the existence of autopolyploidy.

9. FESTUCA OVINA L. VAR. BREVIFOLIA (R. BR.) HART.

The chromosome number of *F. ovina* previously given by various authors is cited on p. 268. The var. *brevifolia* under discussion was

found to be a tetraploid with the number 2n = 28 (Fig. 33). A complete morphological analysis of the chromosomes was possible, the result of which showed that the chromosome complement consists of four morphologically homologous genomes, each of the 7 types (Fig. 34) being represented 4 times. Thus var. *brevifolia* is at least from a chromosome morphological point of view to be regarded as an autopolyploid. Detailed data concerning the morphology of the chromosomes are given in Table 3 and in the diagram of types in Fig. 34. As appears from Figs. 33 and 34, types *C* and *D* are strikingly alike; the difference in total length between the two chromosomes as well as the difference between the relative lengths of the different segments are

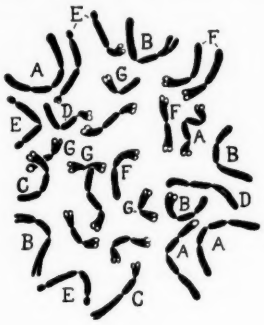
TABLE 3. *The average length of the different chromosome types in Festuca ovina var. brevifolia.*

Type	*A*	*B*	*C*	*D*	*E*	*F*	*G*
Length of the segments in μ	1,5				0,4		
	1,0	1,2	1,3	1,4	1,2		
	1,1	0,8	1,0	0,9	1,7	1,7	1,2
	1,7	2,2	1,8	1,6	0,4	1,8	1,4
Total length in μ	5,3	4,2	4,1	3,9	3,7	3,5	2,6

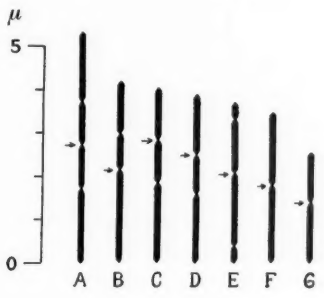
so small that they are within the limits of the expected errors of measurement. The difference between the other types is so great that they can easily be distinguished from one another.

If a comparison is made between the metaphase drawing reproduced in Fig. 26 from *F. rubra* var. *arenaria* and that in Fig. 33 from *F. ovina* var. *brevifolia,* and between Tables 2 and 3 and again between the diagrams of types in Figs. 27 and 34, a rather conspicuous difference between the morphology of the chromosomes in the two species can be ascertained. The characteristic short intercalary segment in the *A* type chromosomes in *F. rubra* var. *arenaria* is missing in chromosomes of the *A* type in *F. ovina* var. *brevifolia.* Our attention was especially drawn to this feature owing to the fact, as will be shown later, that a similar short intercalary segment was also found in the *A* type chromosomes of the diploid *F. ovina* from arctic Norway and is, moreover, present in the *A* type described by RANCKEN (1934) in *F. pratensis.* A series of good metaphase plates from different

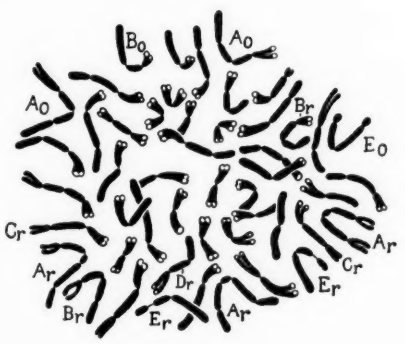
preparations and individuals of *F. ovina* var. *brevifolia* were carefully studied, but no indication of such a segment could be discovered. Further, there is another distinctive difference between the *A* type



33



34



35

Figs. 33 and 34. *Festuca ovina* v. *brevifolia*, 2n = 28. — Fig. 33, somatic metaphase plate, most types can be seen represented four times. — Magnification: 3600 ×. — Fig. 34, diagrammatic representation of the chromosome types present in the somatic complement. The *C* and *D* types are very similar in appearance. The primary constrictions are indicated by arrows.

Fig. 35. Somatic metaphase plate of *Festuca ovina* v. *vivipara*, 2n = 49. The indices *o* and *r* in addition to the usual capital letters indicate that the chromosomes in question are morphologically homologous to those found in *F. ovina* v. *brevifolia* and in *F. rubra* v. *arenaria* respectively. — Magnification: 3600 ×.

chromosomes of these two species in respect to the relative length of the different segments. The distal segments in the *A* type chromosomes in *F. ovina* var. *brevifolia* are considerably longer than the

proximal ones, but in *F. rubra* var. *arenaria* the position is reversed, the distal segments of the *A* type chromosomes in this species being the shortest and the following proximal segments the longest. Another characteristic type of chromosomes in *F. ovina* var. *brevifolia* is the *E* type. As in the *A* type, chromosomes of this type also consist of four segments, but the distal segments are very short and are spherical in shape (cf. Fig. 33).

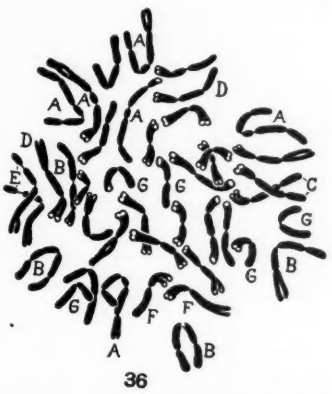
10. FESTUCA OVINA L. VAR. VIVIPARA L.

As already mentioned above, TURESSON (1930, 1931) found the chromosome numbers $2n = 21$, 28 and 42 in the viviparous forms of *F. ovina* from Scandinavia investigated by him. The var. *vivipara* from Spitsbergen investigated here was found to have the number $2n = 49$ (Fig. 35). The chromosome number alone is sufficient reason for assuming that we have here the product of a cross, and the parents must have had different chromosome numbers. The result of the chromosome morphological examinations showed that the 49-chromosome form is of allopolyploid origin, since more than 7 different types of chromosomes can be distinguished and the number of the most characteristic and comparatively easily identifiable types present never corresponded to the number of genomes. The chromosomes marked *Ao* in Fig. 35 are in all respects similar to the *A* type chromosomes found in *F. ovina* var. *brevifolia*. The maximum number of chromosomes of this type found in var. *vivipara* was four. Likewise, chromosomes exactly like the easily identifiable *E* type chromosomes in *F. ovina* var. *brevifolia* were found to be present in var. *vivipara*, but the number of such chromosomes could not be determined for certain, still it can be said that the number can hardly be more than four. A chromosome of this type, marked *Eo*, can be seen in the periphery, at 3 o'clock, of Fig. 35.

A more interesting point, however, is that in the chromosome complement in this form of *F. ovina* var. *vivipara* there are chromosome types which are morphologically exactly like the *A* and *E* types previously described as characteristic of *F. rubra* var. *arenaria*. The *A* type chromosomes with their short intercalary segments were never present to a greater number than three in the form under discussion. In Fig. 35 all three of these chromosomes, marked *Ar*, can be very distinctly seen. Further, in the same figure we see quite plainly another two chromosomes, marked *Er*, which are morphologically homologous with the *E* type chromosomes found in *F. rubra* var.

arenaria. The correct number of chromosomes of this type present could not, however, be determined for certain. Other chromosome types, which may be said to be morphologically homologous with those found in *F. rubra* var. *arenaria*, were met with (cf. Fig. 35), but it was not possible to determine the number of chromosomes of these types for certain. Primary importance is, however, attached to the more distinctive types *Ar* and *Ao* and *Er* and *Eo*. That chromosomes of these types are morphologically quite in conformity with the *A* and *E* types of chromosomes present in *F. rubra* var. *arenaria* and *F. ovina* var. *brevifolia* respectively will be quite evident from close comparison of these chromosomes in Figs. 26, 27, 33 and 34 with those in Fig. 35.

It may be mentioned that all traces of sexual organs were entirely missing in the individuals examined by the present writer. SCHOLANDER (1934) says that in the high Arctic this viviparous *Festuca* appears practically always to have totally lost the last trace of rudiment of sexual organs.



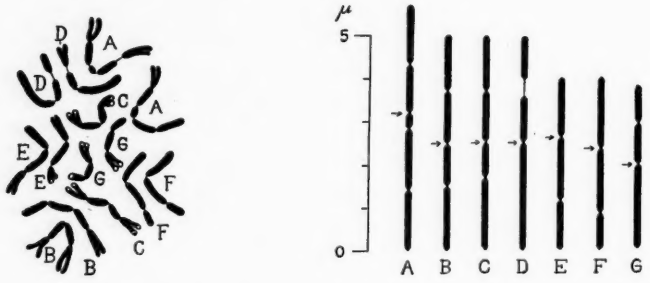
36

Fig. 36. Somatic metaphase plate of *Festuca rubra* v. *arenaria* from Tromsö, Norway, 2n = 42. The morphology of the chromosomes is the same as that of the v. *arenaria* from Spitsbergen (compare Figs. 26 and 27). In this plate, too, all the six *A* type chromosomes are quite clear. — Magnification: 3600 ×.

In connection with the investigations presented above, material of *F. rubra*, *F. ovina* and *F. ovina* var. *vivipara* from arctic Norway was collected for the purpose of studying their chromosome numbers and the chromosomal morphology. The material was collected from the districts round Tromsö and Narvik. The *F. rubra* commonly occurring in these districts must most likely be referred to var. *arenaria*. The chromosome number is the same as in *F. rubra* var. *arenaria* from Spitsbergen (2n = 42). Morphologically, no conspicuous difference could be discerned between the chromosomes of the two forms. What has previously been said concerning the chromosome morphology of *F. rubra* var. *arenaria* from Spitsbergen thus holds good for the form of *F. rubra* from arctic Norway. For the sake of comparison a metaphase plate was drawn and is reproduced in Fig. 36, which shows

various chromosome morphological details. Among other things, all six chromosomes of the *A* type can be identified.

In *Festuca ovina* from these localities the chromosome number was found to be the same as that found by TURESSON (1930) for the sexual forms of this species from other localities in Scandinavia, *viz.* 2n = 14. Besides being a diploid, *F. ovina* differs quite considerably in a chromosome morphological respect from *F. ovina* var. *brevifolia*. As will be seen from Figs. 37 and 38, the *A* type chromosomes have a short intercalary segment corresponding to that in the *A* type chromosomes in *F. rubra* var. *arenaria*. As in the latter species, the *A* type chromosomes in *F. ovina* also consist of five segments, but there is a certain



37 38

Figs. 37 and 38. *Festuca ovina* from Tromsö, Norway, 2n = 14. — Fig. 37, somatic metaphase plate; the morphology of all the chromosomes is clear, each type is represented twice. Note the somatic pairing. — Magnification: 3600 ×. — Fig. 38, diagrammatic representation of the chromosome types present in the somatic complement. Types *B* and *C*, together with *E* and *F*, have approximately the same appearance. The primary constrictions are indicated by arrows.

difference in respect to the relative lengths of the segments (cf. Tables 2 and 4). Other chromosomes, too, resemble those found in *F. rubra* var. *arenaria* very closely in appearance. But the chromosomes in *F. ovina* are on the average longer. As far as the *G* type chromosomes are concerned, this difference in length is very great (1,4 μ). Chromosomes of the *G* type in *F. ovina* have besides a secondary constriction. No secondary constriction was observed in the *G* type chromosomes in var. *brevifolia* and *F. rubra* var. *arenaria*. Chromosomes of type *D* always had, practically speaking, a long secondary constriction, as appears in Fig. 37 (cf. also Plate I, Fig. 1). Apart from the difference in length,

this type is conspicuously like the type *E* chromosomes in *F. rubra* var. *arenaria.*

A close examination of the diagram of types (Fig. 38) will show that types *B* and *C* are strikingly alike as regards segmentation, the relative lengths of the different segments and the position of the primary constriction. The total length was found to be exactly the same (cf. Table 4). Likewise, types *E* and *F* closely resemble each other. In this respect *F. ovina* constitutes an analogy to *Calamagrostis neglecta,* in which the same circumstance with two and two approximately similar chromosomes were observed, so that there is a certain justification in classifying the chromosomes into 5 types instead of 7.

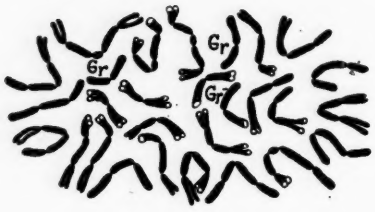
TABLE 4. *The average length of the different chromosome types in Festuca ovina.*

Type	*A*	*B*	*C*	*D*	*E*	*F*	*G*
Length of the segments in μ	1,4						
	1,2	1,3	1,3				
	0,3	1,2	1,2	0,9	1,3	1,6	0,9
	1,4	1,0	0,8	1,1	1,5	1,5	0,9
	1,4	1,5	1,7	2,5	1,2	0,9	2,0
Total length in μ	5,7	5,0	5,0	4,5	4,0	4,0	3,8

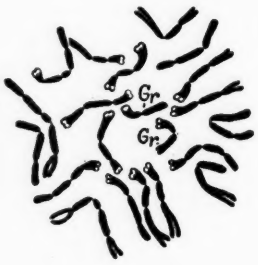
Somatic pairing was frequently observed in *F. ovina.* Such a tendency to somatic pairing will be seen in Fig. 37.

The viviparous *F. ovina* from the above-mentioned localities occurs in two habitually quite different forms. One of them, which is as a rule very robust and highly viviparous, was always found to have the chromosome number $2n = 28$ (Fig. 39). According to the observations made by the present writer, this 28-chromosome form seems to be very common in these regions, both on the islands and on the mainland. In the other form, which can best be characterized as semi-viviparous, there occur simultaneously in the inflorescences both fully developed phenotypical non-viviparous $\pm$ fertile flowers as well as viviparous, sterile flowers. This form was found to be a triploid with the chromosome number $2n = 21$ (Fig. 40). These chromosome numbers are fully in accord with those given by TURESSON (1930, 1931) for the wholly or semi-viviparous forms investigated by him.

The purpose of this investigation, however, was to try to find out whether these viviparous forms of *F. ovina* were also of allopolyploid origin, which may be regarded as certain in the case of the previously mentioned 49-chromosome form from Spitsbergen, and moreover whether, in the event of allopolyploidy, there are chromosome types which are morphologically homologous with those found in *F. ovina* and other types morphologically homologous with those met with in *F. rubra* var. *arenaria*. As already pointed out, *F. ovina* and *F. rubra* var. *arenaria* have much in common as far as the morphology of the chromosomes is concerned. But there is nevertheless a very obvious differ-



39



40

Figs. 39 and 40. *Festuca ovina* v. *vivipara* from Tromsö, Norway. — Fig. 39, somatic metaphase plate of a viviparous form with $2n = 28$. — Fig. 40, somatic metaphase plate of a semi-viviparous form with $2n = 21$. — In both plates the chromosomes, which are found to be morphologically homologous to the *G* type chromosomes of *F. rubra* v. *arenaria*, are marked *Gr*. — Magnification: 3600 ×.

ence between the two species in respect to the *G* type chromosomes. The best preparations were obtained from the 28-chromosome form, and in the chromosome complement of this form there occurred a type, differing widely from all other types, which was not represented more than three times. This gives good grounds for assuming that we have here a case of allopolyploidy. In Fig. 39 all three chromosomes, marked *Gr*, are visible. Morphologically, these chromosomes are homologous with the *G* type chromosomes in *F. rubra* var. *arenaria*. No corresponding type was found in the diploid *F. ovina*.

The fixed preparations of the 21-chromosome, semi-viviparous form were not as suitable as they should be for chromosome morphological analysis. On that account it must be subjected to a more thorough investigation on a future occasion. On the basis of the available material

it can be concluded that this form, too, is in all probability an allopolyploid, since a chromosome corresponding to the above-mentioned *Gr* type, which was not observed in *F. ovina*, seems to be present. It was not possible to determine the number of chromosomes of this type for certain, but at any rate the number is not higher than two, as appears from Fig. 40, where the chromosomes which may be said to belong to this type are marked *Gr*.

11. HIEROCHLOE ALPINA (LILJEBL.) ROEM. ET SCHULT.

This species is an octoploid with the chromosome number 2n = 56 (Fig. 41). In *H. odorata*, AVDULOV (1931) found the number 2n = 42, and KATTERMANN (1932) the number 2n = 28.

No attempt was made to perform detailed examinations of the morphology of the chromosomes, but it may be mentioned that a large number of the chromosomes were seen to have, in addition to the invariably well-defined primary constriction, one or more secondary constrictions (cf. Fig. 41), as is the case in all other arctic grasses dealt with in this paper.

41

Fig. 41. Somatic metaphase plate of *Hierochloe alpina*, 2n = 56. — Magnification: 3600 ×.

12. PHIPPSIA ALGIDA (SOLAND.) R. BR.

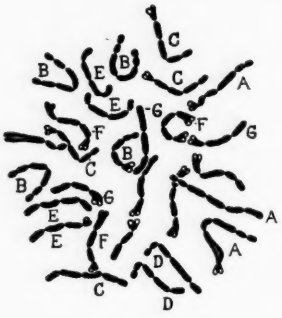
The chromosome number in *Ph. algida* is 2n = 28 (Fig. 42 and Plate I, Fig. 3). The morphology of the chromosomes was carefully studied and it was found that the chromosome complement is made up of 7 different chromosome types, the number of each type being four. Along with Fig. 42, Table 5 and diagram of types, Fig. 45, clearly show the chromosome morphological data. In view of the fact that the chromosome complement is composed of four morphologically homologous genomes, it is reasonable to assume that *Ph. algida* is an autotetraploid.

TABLE 5. *The average length of the different chromosome types in Phippsia algida.*

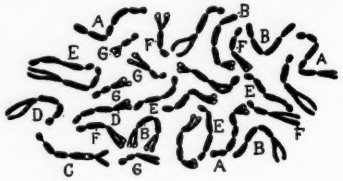
Type	*A*	*B*	*C*	*D*	*E*	*F*	*G*
Length of the segments in μ	0,4	0,4					
	0,5	0,4	0,5	0,3			
	1,2	0,9	0,6	0,4	0,6	0,6	
	0,6	1,0	0,7	0,7	0,8	0,6	0,8
	1,3	0,5	1,0	1,1	0,8	0,8	0,8
	0,7	0,4	0,6	0,5	0,6	0,8	0,9
Total length in μ	4,7	3,6	3,4	3,0	2,8	2,8	2,5

13. PHIPPSIA CONCINNA (TH. FR.) LINDEB.

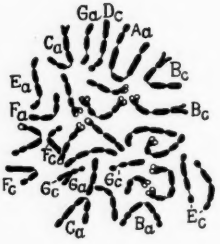
Like *Ph. algida*, this species is a tetraploid having the chromosome number 2n = 28 (Fig. 43). As regards the morphology of the chromo-



42



43



44

Figs. 42—44. Somatic metaphase plates of the *Phippsia* species. — Fig. 42, *Ph. algida*, 2n = 28; the chromosome types *B*, *C* and *E* can be identified to the number of four. — Fig. 43, *Ph. concinna*, 2n = 28; the chromosome types *B*, *E*, *F* and *G* can be identified to the number of four. — Fig. 44, *Ph. concinna* v. *algidiformis*, trisomic type, 2n = 29. The capital letters with the indices *a* and *c* indicate that the chromosomes in question are found to be morphologically homologous to those marked by the same capital letters in *Ph. algida* (Figs. 42 and 45) and in *Ph. concinna* (Figs. 43 and 46). — Magnification: 3600 ×.

somes a few types very closely resemble those in *Ph. algida*. A comparison of the diagrams of the types (Figs. 45 and 46) will show that the *A* type chromosomes in both species are essentially alike with the exception of a difference in the total length. There is also a difference in length between chromosomes of the other types (cf. Tables 5 and 6). Further, from the diagrams of types it will be seen that there is no essential difference between the type *C* chromosomes in *Ph. concinna* and the *D* type chromosomes in *Ph. algida*. In *Ph. concinna* chromosomes of this appearance, according to their length in proportion to the others, rank as No. 3, while in *Ph. algida* they are No. 4, for which reason they are denoted by different letters in the two cases.

TABLE 6. *The average length of the different chromosome types in Phippsia concinna.*

Type	*A*	*B*	*C*	*D*	*E*	*F*	*G*
Length of the segments in μ	0,3						
	0,4		0,3				
	1,0	0,8	0,5	0,3	0,3		
	0,5	0,9	0,9	0,6	1,0	0,4	0,3
	1,0	0,9	0,9	0,8	0,9	0,6	0,4
	0,7	0,9	0,6	1,3	0,5	1,7	1,0
Total length in μ	3,9	3,5	3,2	3,0	2,7	2,7	1,7

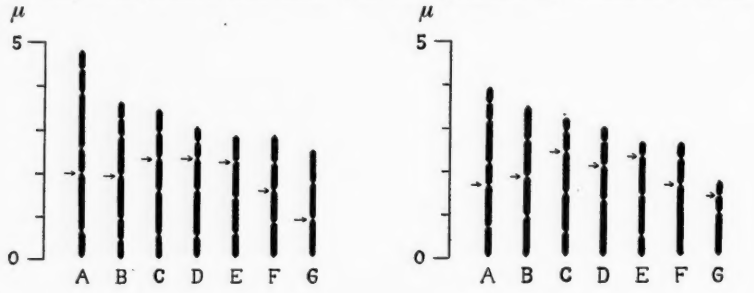
The chromosomes most easily identifiable are those of type *G*. These differ sharply from the other types on account of their being considerably shorter and also by reason of the terminal position of the primary constriction (cf. Fig. 46). The number of chromosomes of each of the types exemplified in Fig. 46 was found to be four. *Ph. concinna*, like the preceding species, *Ph. algida*, must therefore be regarded, at least from a chromosome morphological point of view, as an autotetraploid.

14. PHIPPSIA CONCINNA (TH. FR.) LINDEB. VAR. ALGIDIFORMIS (SMITH) HOLMB.

According to H. SMITH (1914), the new subspecies of *Ph. concinna* (the subsp. *algidiformis*) set up by him occupies an intermediate position between *Ph. algida* and *Ph. concinna*, and he remarks (l. c., p. 251):

»Es ist nicht unmöglich, dass dieselbe hybridogener Natur ist, was in diesem Falle jedoch nur eine Vermutung sein kann». In addition to Scandinavia, the above author mentions this subsp. *algidiformis* from several localities in Spitsbergen and among other places from Advent Bay, where the present writer collected the main part of his material of *Phippsia*.

Later, HOLMBERG (1924) treated the genus *Phippsia* very closely and made a critical study of SMITH's herbarium material. A type, differing somewhat from *Ph. concinna*, having a narrow apex, and short, erect and compressed branches, was distinguished by HOLMBERG from



45 46

Figs. 45 and 46. Diagrammatic representation of the different chromosome types present in the somatic complements of the species of *Phippsia*. — Fig. 45, *Ph. algida*. — Fig. 46, *Ph. concinna*. — The primary constrictions are indicated by the arrows.

the main form as var. *algidiformis* (H. SMITH) HOLMB.—SMITH's herbarium material was found by HOLMBERG to be mostly a mixture of *Ph. algida* and *Ph. concinna*, and the latter consisted mainly of the above-mentioned aberrant type, var. *algidiformis*. HOLMBERG does not agree with SMITH that this type can be considered to occupy an intermediate position between the two *Phippsia* species, *algida* and *concinna*, and in his opinion it can hardly be regarded as a hybrid. He says (l. c., p. 132): »Eine Herabsetzung in der Entwicklung der männlichen oder weiblichen Organe ist nicht zu konstatieren. Dazu kommt, dass in Härjedalen und Jämtland, wo SMITH selbst so genaue Untersuchungen vorgenommen hat, noch keine *Ph. algida* gefunden wurde, und dass andererseits aus schwedischem Lappland, wo man nach SMITH das Vorkommen von *Ph. concinna* erwarten könne, gleichfalls noch kein Exemplar von dieser Art nachgewiesen worden ist».

Contrary to var. *algidiformis*, the hybrid between the two species described by HOLMBERG, and which was in his opinion a true hybrid,

is quite sterile with only about 5 per cent good pollen (cf. also HOLMBERG, 1926). It is therefore reasonable that, in view of the good fertility in var. *algidiformis*, he does not find any grounds for assuming that this form is a hybrid.

The material collected in Spitsbergen was quite fertile. Mr. LID, Curator of the Botanical Museum, Oslo, who has subjected this material to a critical examination, states that it agrees very well with HOLMBERG's var *algidiformis*. Only one typical specimen was available for cytological analysis and the chromosome number of this individual was found to be $2n = 29$ (Fig. 44), thus a trisomic plant. Hence no support for either of the above-mentioned views advanced by SMITH (l. c.) and HOLMBERG (l. c.) can be obtained from the chromosome number. Of greater interest is the result of the chromosome morphological examination, which indicates that we have here a case of allopolyploidy, in contradistinction to what was found in the previously mentioned species, *Ph. algida* and *Ph. concinna*, in which the chromosome complement consists of four morphologically homologous genomes and are therefore probably autopolyploids. In the var. *algidiformis* under discussion there occur two chromosomes corresponding to the characteristic *G* type chromosomes in *Ph. concinna*. In Fig. 44 both these chromosomes, marked *Gc*, are very plainly seen. Chromosomes of this type are so easily recognisable that their number can be determined with absolute certainty, and in a series of good metaphase plates this number was always found to be two. Chromosomes of another type, at least equally characteristic and easily identifiable, are those designated with *Ga* in Fig. 44. These short chromosomes with their approximately equally long segments are conspicuously like the *G* type of chromosomes in *Ph. algida* in appearance and must be assumed to be homologous with them. The number of chromosomes of this type present in var. *algidiformis* is also two. As appears from the diagram of types (Fig. 46), there is no corresponding type present in *Ph. concinna*.

As already pointed out, *Ph. algida* and *Ph. concinna* have also certain types of chromosomes which are very similar in appearance and are therefore difficult to distinguish from one another in a hybrid such as we are evidently faced with in this case. But in addition to the *G* type chromosomes mentioned, there are also a few other types which are characteristic of *Ph. algida* and others again characteristic of *Ph. concinna* (compare Fig. 44 with the diagrams of types, Figs. 45 and 46). There are therefore adequate reasons for assuming that the

var. *algidiformis* under discussion is really a hybrid between *Ph. algida* and *Ph. concinna.*

The good fertility of this hybrid, which seems to be quite equal to that of the parent species, is especially interesting. As already mentioned, the parent species must, in accordance with the chromosome morphological conditions, be regarded as autopolyploids. Further evidence in support of the occurrence of autopolyploidy is furnished by the fact that the tetraploid hybrid is quite fertile. We have here an analogous case with that surmised by FAGERLIND (1934) concerning the hybrid *Galium Mollugo* × *verum* (= *G. ochroleucum* WOLFN.) FAGERLIND calls attention to the fact, to which little consideration has been given by cytologists and geneticists, that in genera with a considerable interspersion of autopolyploids new allopolyploid species may arise in crosses already in F_1 and that constancy and good fertility may be attained without any chromosome doubling being necessary. In accordance with FAGERLIND's scheme the case of *Phippsia* could be illustrated by designating the four genomes in each of the autotetraploid species, *Ph. algida* and *Ph. concinna*, *AAAA* and *CCCC* respectively. Consequently the hybrid must then be designated *AACC*. But that is exactly the same result as would be obtained by crossing two diploid species of the constitution *AA* and *CC*, which in F_1 will give the hybrid *AC*, which in a subsequent chromosome doubling will produce a constant and fertile allotetraploid of the constitution *AACC*. The only difference is that in one case a chromosome doubling takes place in the parents of the hybrid, while in the other case a chromosome doubling occurs in the hybrid itself, thus in conformity with the scheme by which new constant and fertile allopolyploids are supposed to arise.

The indivduals of the two *Phippsia* species examined by the present writer were all tetraploids, but it is quite probable that diploids may nevertheless still exist and that the sterile hybrid described by HOLMBERG (l. c.) is only a cross between two diploids or between a diploid and a tetraploid. In both cases a more or less pronounced sterility is to be expected. This is of course simply an assumption and it must therefore be left to future cytological investigations to throw light on the problem raised by the said sterile hybrid.

With regard to the hybrid examined here, *Ph. algida* × *Ph. concinna*, it may be mentioned that the chromosomes were found to be considerably shorter in length than those of the parent species, but the constrictions are, however, just as clearly defined as in the latter (cf. Figs. 42—44). The difference can therefore hardly be thought to be

due to bad fixation. The measurements were performed in cells from corresponding tissues in both parent species and the hybrid. Chromosomes of the types that could be identified were on the average about 20 per cent shorter in the hybrid than in the parents and a corresponding difference in length seems to exist between all chromosomes of the complement — both those from *Ph. algida* and also those from *Ph. concinna*. It is possible that this is only a question of an individual difference which could not be thoroughly investigated owing to insufficient material, but it is just as probable that this difference in length is caused by the hybridisation itself, as has been shown, for instance, in certain *Crepis* hybrids (NAVASHIN, 1928, 1934). All alterations occurring in the chromosome complement brought about by hybridisation are termed »amphiplasty» by NAVASHIN. This condition is again subdivided by the same author (NAVASHIN, 1934, p. 198) as follows: ». . . a) sporadic amphiplasty distinguished by its chance occurrence and including the various chromosome reorganisations (dislocations) which seem to be stimulated by the hybrid conditions; b) regular amphiplasty which invariably occurs in a given interspecific combination. This in turn includes differential amphiplasty which affects only individual chromosomes, and neutral amphiplasty which is manifested in all the chromosomes of a given set».

In the hybrid *Ph. algida* × *Ph. concinna* we have an instance of neutral amphiplasty. The alteration is, however, along identical lines in that the chromosomes of both the parent species are shortened. In this respect conditions are quite different from those instances mentioned by NAVASHIN in *Crepis* hybrids, where the change did not in any instance proceed in the same direction, but, on the contrary, one specific set showed shortening while the other was lengthened.

Judging from the literature, no satisfactory, generally accepted explanation of this phenomenon has been offered. The main point in this connection, however, is that such changes as those mentioned have been shown for certain in experimentally produced hybrids, namely in *Crepis* (NAVASHIN, l. c.). The differences observed in the length of the chromosomes in *Phippsia*, between the hybrid and the supposed parent species, do not therefore invalidate the evidence afforded by the other chromosome morphological characteristics.

15. POA ABBREVIATA R. BR.

As a rule *Poa* is a most unsuitable object for detailed cytological investigations, for even a simple determination of the number of chro-

mosomes is often impossible (cf. MÜNTZING, 1933 a, and RANCKEN, 1934). »Da die Chromosomen bei *Poa* ziemlich zahlreich und ausserdem meist in den Wurzelspitzen stark aneinandergedrängt sind, sodass sie mehr oder weniger den ganzen Zellraum einnehmen, und dazu noch lang und ineinander verflochten sind, kann ihre Anzahl nur selten in den Metaphasenplatten gezählt werden» (RANCKEN, l. c., p. 43).

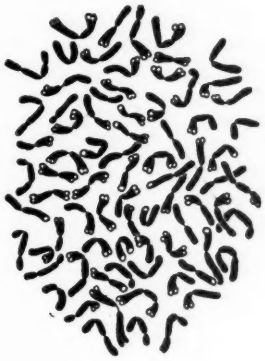
The chromosome numbers in the arctic *Poa* species seem, throughout, to be very high and the difficulties encountered in attempting to determine the number exactly are therefore rather great. In spite of repeated control counts the numbers must be given approximately as far as one or two species are concerned. One of these species is *Poa abbreviata* with the number $2n = 76\pm$. Two habitually somewhat different types were studied, both of which seemed to have the same chromosome number. The number of chromosomes found in different metaphase plates and from different preparations varied between 73 and 77. Still the aneuploid number, $2n = 76$, is probably the correct one, since this number was found in the absolutely best plates for counting. A plate, which under the circumstances must be characterized as good and which shows 76 chromosomes, is reproduced in Fig. 47.

16. POA ALPIGENA (E. FRIES) LINDM.

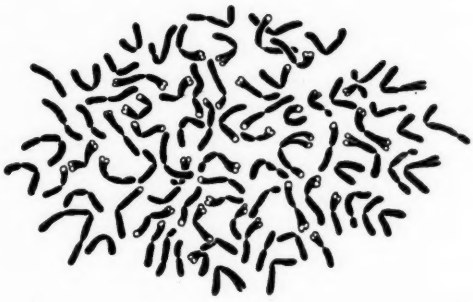
Two fairly different types of this species were examined. One of them — of the *iantha* type (v. LINDMAN, 1926) — was found to have the chromosome number $2n = 77\pm$ (Fig. 48), while the other — which was of the *domestica* type — had the number $2n = 84$ (Fig. 49). The length of the chromosomes varies between about 4,0 and about 1,6 μ. These are practically the same figures as those recorded by RANCKEN (l. c.) for the closely related species *Poa pratensis*, *viz.* approximately 4,0 and 1,5 μ for the longest and the shortest chromosomes respectively.

The course of meiosis in both the above-mentioned types is generally extremely irregular. Thus well organised metaphase plates were observed only by way of exception. A frequently very large number of univalents could be discerned lying scattered about in the plasm outside the plate. In side view of anaphase I a larger or smaller number of univalents could be regularly seen lagging. Sometimes a few of these univalents divide longitudinally at the first division, but generally they do not divide and then after an entirely random distribution they move towards the two poles. Fig. 52, from the 84-chromosome *domestica* type, shows a commonly observed anaphase I picture in which several

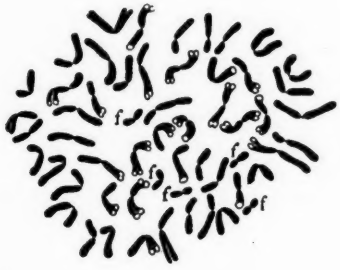
47



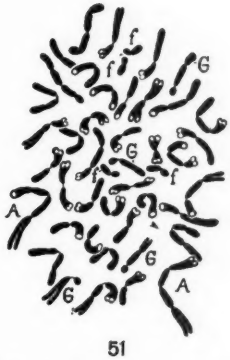
48



49



50



51

Figs. 47—51. Somatic metaphase plates of different *Poæ*. — Fig. 47, *P. abbreviata,* plate showing 76 chromosomes. — Fig. 48, *P. alpigena, iantha* type, plate showing 77 chromosomes. — Fig. 49, *P. alpigena* of *domestica* type, $2n = 84$. — Fig. 50, *P. alpigena* v. *colpodea,* $2n = 51 + 5ff$. — Fig. 51, *P. alpigena* v. *vivipara,* $2n = 42 + 4ff$. Only two chromosomes of the *A* type and four of the *G* type are to be found in this complement. — Magnification: 3600 ×.

chromosomes are lagging; three univalents are on the point of dividing. Similar conditions with respect to the behaviour of the univalents at first division seem to occur also in *Poa cæsia*, where the univalents sometimes divide during first division and occasionally they possibly do not divide (KATTERMANN, 1930). — At interkinesis micronuclei were less frequent, which indicates that both products of division and unsplit univalents reach the two poles in time to be able to participate in the formation of the new daughter nuclei. Like the first division, the course of the second division is also abnormal to a high degree. At metaphase II a larger or smaller number of chromosomes could be seen lying scattered outside the plate, and at anaphase II there appeared numerous lagging chromosomes. But contrary to the state of things at anaphase I, a large number of the lagging chromosomes at anaphase II very often do not seem to reach the poles in time to be included in the new daughter nuclei. Consequently pentads, hexads, etc. could frequently be observed in the tetrad stage. Fig. 53, again from the 84-chromosome *domestica* type, shows a hexad. No restitution nuclei (cf. ROSENBERG, 1926 a, 1926 b, 1927) were observed, but since dyads and giant pollen grains were not rare it must be assumed that restitution nuclei occur. It may be mentioned that the finished pollen looked morphologically good, but as was to be expected, in view of the above-mentioned irregularities during meiosis, the pollen varied very much in size.

The irregular course of meiosis and the variable size of the pollen, mentioned above, furnish good reasons for assuming that gametes with quite different chromosome numbers are produced in *Poa alpigena*. These gametes with different numbers of chromosomes can also be assumed to function normally, as the pollen, as already mentioned, was morphologically normal. One should therefore expect progenies with variable chromosome numbers, as for instance in certain biotypes of *Poa alpina* (v. MÜNTZING, 1933 a), but that does not seem to be the case. Progenies of the 84-chromosome type were raised in the summer of 1936, of which 10 plants were selected at random for determination of the chromosome number. Of these plants, 4 individuals gave unsatisfactory preparations so that their chromosome numbers could not be determined for certain, but the counts seemed to indicate that the correct number was $2n = 84$. In the other 6 individuals, from which better fixations were obtained, the number of chromosomes could be determined for certain to be 84 — that is the same number as in the mother plant. In spite of the somewhat scanty material for observation

it may be said that in all probability the *Poa alpigena* under discussion here propagates by apomictic seed-formation. This is further supported by the fact that the progeny possesses a strict uniformity.

17. POA ALPIGENA (E. FRIES) LINDM. VAR. COLPODEA (TH. FRIES) SCHOLANDER.

Of this sterile viviparous *Poa*, two somewhat different types were also examined. One of them had greatly reduced spikelets and was otherwise very abnormal in appearance, being in a marked pathological condition. Both types had the same chromosome number, $2n = 51 + 5ff$ (Fig. 50). The normal chromosomes as well as the fragments were in both cases of the same length and appearance otherwise.

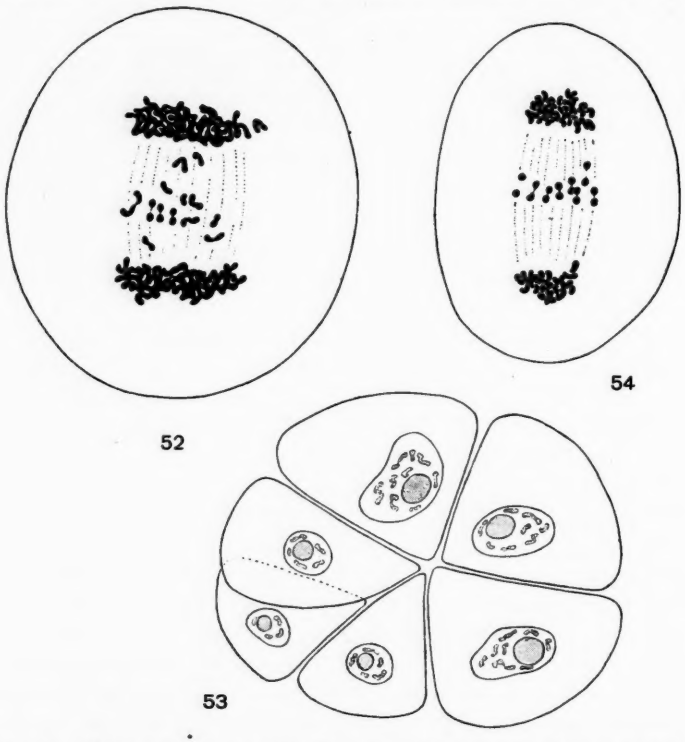
18. POA ALPIGENA (E. FRIES) LINDM. VAR. VIVIPARA (MALMGR.) SCHOLANDER.

The somatic chromosome complement was studied in two morphologically very similar individuals. Both individuals had the chromosome number $2n = 42 + 4ff$ (Fig. 51). Partly owing to the relatively low chromosome number present and partly owing to the conspicuously different appearance of a few chromosomes from the great majority, it was possible to obtain certain chromosome morphological data of interest. The chromosomes which differ most widely from the others are those marked *A* and *G* respectively in Fig. 51. Chromosomes of the *A* type are represented twice; they have submedian primary constrictions and have besides a secondary constriction in each arm so that they consist of four segments. The average length of the *A* type chromosomes is $4{,}4\,\mu$, while the chromosomes next in length measure on the average $3{,}2\,\mu$. This difference in length is so great that the *A* type chromosomes can hardly be confused with other types of chromosomes. The *G* type chromosomes are represented four times. These chromosomes are easily distinguished on account of the subterminal position of the primary constriction (v. Fig. 51), and they also have a secondary constriction in the long arm, nearer the distal end. Chromosomes of this type were also observed in the two types of non-viviparous *Poa alpigena* (v. Figs. 48 and 49), but it was not possible to determine their number in these species.

Thus, considering the chromosome morphological conditions mentioned above, the *Poa alpigena* var. *vivipara* under discussion must be regarded as an allohexaploid.

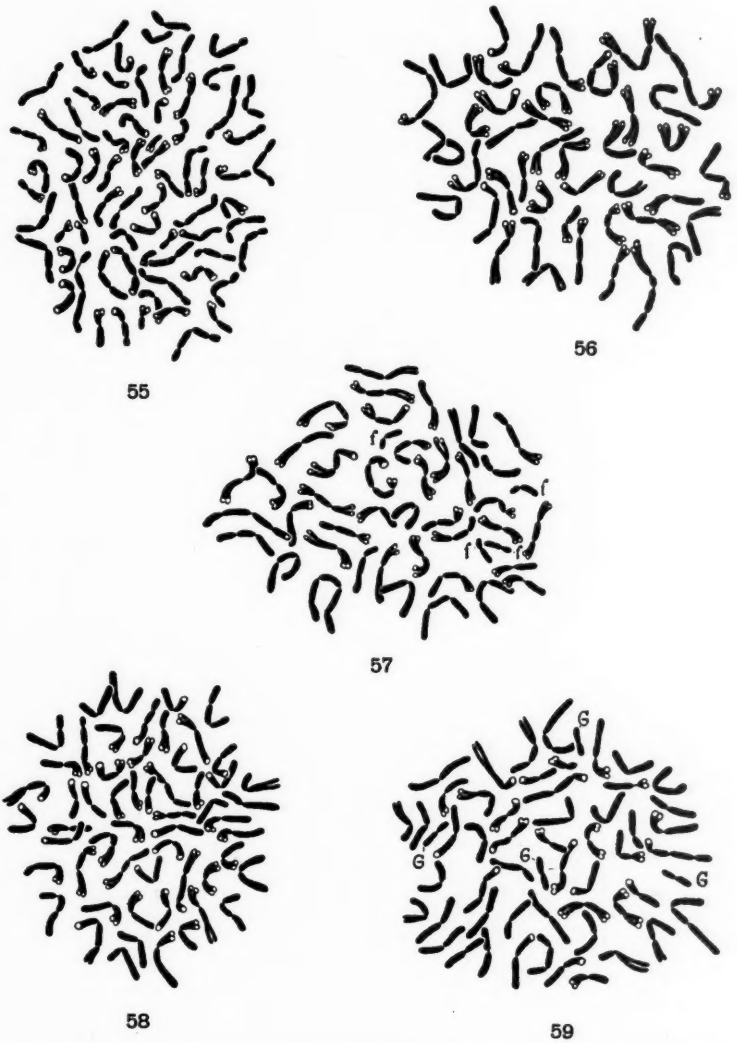
The behaviour of the chromosomes at meiosis must be characterized

as exceedingly abnormal. In side view of metaphase I a great many univalents could frequently be observed outside the plate (Plate I, Fig. 11), and at anaphase I these univalents are lagging. Most frequently these univalents divide in the first division, as shown in Fig. 54.



Figs. 52—54. Meiosis in *Poa alpigena* (Figs. 52 and 53) and *P. alpigena* v. *vivipara* (Fig. 54). — Fig. 52, side view of an anaphase I of the 84-chromosome *domestica* type; several lagging univalents, three of which divide. — Fig. 53, hexad of the same type as above. — Fig. 54, side view of anaphase I of *P. alpigena* v. *vivipara;* all the lagging univalents divide. — Magnification: 2700 ×.

Many of these split univalents reach the pole in time to be included in the two daughter nuclei. In those cases in which both metaphase II plates could be counted, the total number of chromosomes in the two plates was therefore always higher than 46 (42 + 4ff), which was the somatic number. Micronuclei could be observed sometimes at interkinesis, thus indicating that a number of the lagging chromosomes do

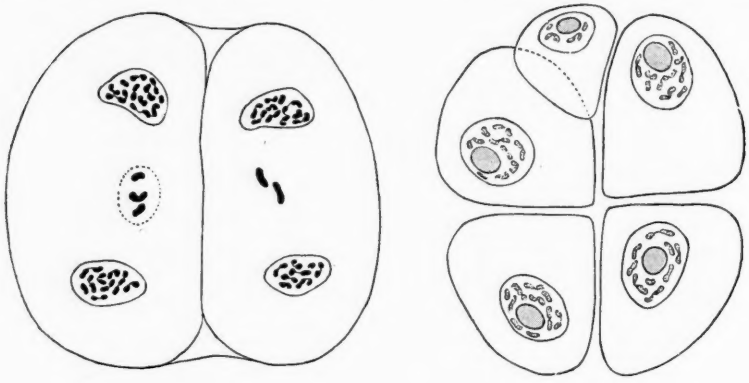


Figs. 55—59. Somatic metaphase plates of different *Poæ*. — Fig. 55, *P. glauca,* plate showing 72 chromosomes. — Figs. 56 and 57, from different biotypes of *P. alpina* v. *vivipara* with the chromosome numbers $2n = 44$ and $2n = 42 + 4ff$ respectively. — Fig. 58, *P. arctica,* $2n = 56$. — Fig. 59, *P. arctica* v. *vivipara,* $2n = 56$, with four very short chromosomes of type *G*. — Magnification: 3600 ×.

not reach the poles in good time. The irregularities recur in the second division as in the previously mentioned non-viviparous *Poa alpigena*, but the pollen was not so good in quality as in the latter, only about 55 per cent of the pollen being morphologically good.

19. POA GLAUCA VAHL.

In this species the number of chromosomes could not be determined exactly. Repeated counts from different preparations and different individuals gave most frequently the number $2n = 72$ (Fig. 55), but in several otherwise well fixed metaphase plates only 70 chromosomes



60 61

Figs. 60 and 61. Meiosis in *Poa glauca*. — Fig. 60, telophase II with lagging chromosomes left out of the new daughter nuclei. — Fig. 61, pentad. — Magnification: 2700 ×.

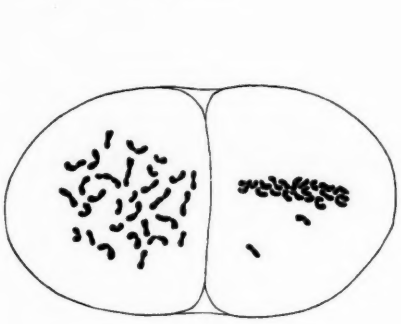
could be counted, and again in other cases 71. AVDULOV (1928) gives the number $2n = 70$ for the *Poa glauca* examined by him.

The course of meiosis in this species is also very irregular. Plate I, Fig. 12 shows the ordinary appearance of anaphase I with lagging chromosomes lying in the spindle between the two poles. The lagging chromosomes as a rule do not pass to the poles in time to be included in the two new daughter nuclei but form micronuclei instead. The irregularities continue through the second division. Fig. 60 shows a telophase II with lagging chromosomes which have been left out of the newly formed nuclei. In the tetrad stage dyads, triads, pentads, etc. could be frequently observed. Fig. 61 shows a pentad. The finished

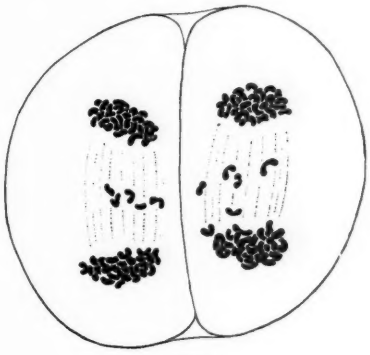
pollen was, however, morphologically good, but varied very much in size.

In conformity with the above-mentioned irregularities at meiosis, the gametes should of course have widely varying chromosome numbers. If *Poa glauca* propagates sexually the progeny should show varying chromosome numbers which are different from the chromosome number of the mother plant. An examination of 7 individuals of the progeny, however, showed that they had the same number as the mother plant, *i. e.* 70—72 chromosomes. But the number most frequently observed in these cases was 70.

Thus, taking everything into consideration, the most probable constant chromosome number gives reason for assuming that the seed-formation is apomictic.



62



63

Figs. 62 and 63. Meiosis in *Poa alpina* v. *vivipara*, from the 44-chromosome biotype. — Fig. 62, metaphase II, the plate in polar view showing 30 chromosomes. — Fig. 63, side view of anaphase II, the univalents which divide at first division are now lagging. — Magnification: 2700 ×.

20. POA ALPINA L. VAR. VIVIPARA L.

MÜNTZING (1933 a) has shown that varying chromosome numbers occur in different biotypes of *Poa alpina*. The same thing can be said to be true of different biotypes of var. *vivipara*. Thus two investigated biotypes from Spitsbergen had the numbers $2n = 44$ (Fig. 56) and $2n = 42 + 4ff$ (Fig. 57). A third biotype from arctic Norway was found to have the number $2n = 33$. STÄHLIN (1929) gave the number $2n = 42$ for the var. *vivipara* he examined. The chromosomes are, throughout, somewhat longer than those in the other species of *Poa*

dealt with in this paper. Apart from the fragments, the length of the longest chromosomes was 4,5 μ and of the shortest chromosomes 2,0 μ. The fragments of the 42-chromosome biotype had an average length of 1,1 μ, otherwise they were similar in appearance.

At meiosis there occur irregularities corresponding to those in the *Poa* species previously described. The univalents most frequently divide at the first division and produce supernumerary chromosomes at metaphase II, as seen in Fig. 62 from the 44-chromosome biotype, one plate (in polar view) showing 30 chromosomes and the other (in side view) 21. In the second division these previously split univalents segregate accidentally, at anaphase II they are most frequently lagging (Fig. 63). The tetrad stage had the same appearance as in *Poa alpigena* and *P. glauca*. Contrary to the case in *Poa alpigena* var. *vivipara*, the finished pollen was, however, morphologically of good quality, about 90 per cent being morphologically normal.

21. POA ARCTICA R. Br.

Three individuals from three different localities were found to have the same chromosome number, $2n = 56$ (Fig. 58).

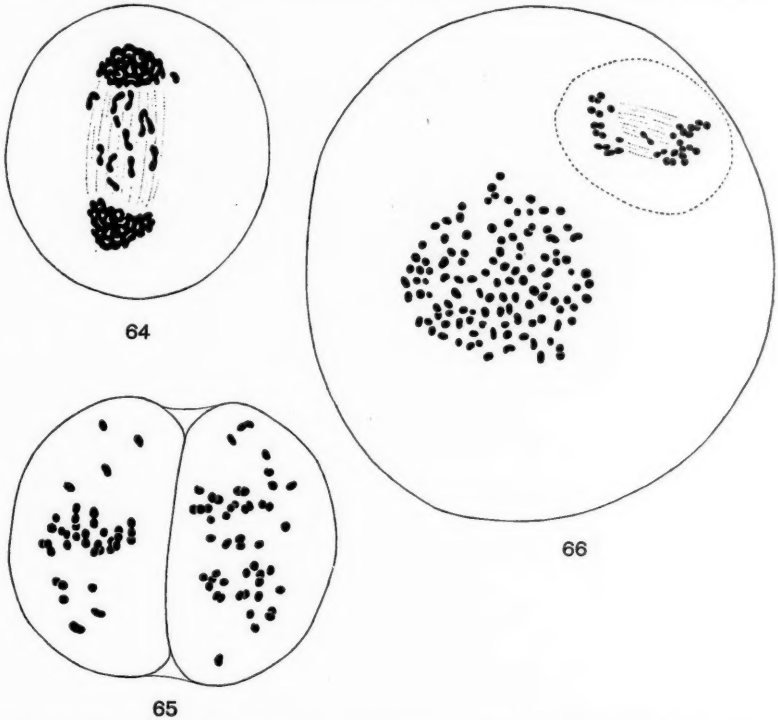
The behaviour of the chromosomes at meiosis conveyed in general the same impression as that in the other *Poa* species. Plate I, Fig. 13 shows two cells at anaphase I with lagging univalents, some of which are on the point of dividing. Micronuclei could very frequently be seen at interkinesis. The second division runs the same irregular course as the first division and in the tetrad stage abnormalities of various kinds occurred. The pollen was quite normal morphologically.

One of the individuals collected was isolated before and during flowering. Seed-setting was very good and of 200 seeds put to germinate 194 germinated. This I_1 material was found to be strictly uniform and an examination of the chromosome number in 5 plants showed that all of them had the same number as the mother plant, *viz.* $2n = 56$. This fact together with the abnormal meiosis of the mother plant indicates very strongly that seed-formation in this species is apomictic.

22. POA ARCTICA R. Br. var. VIVIPARA (Malmgr.) Scholander.

The chromosome number was found to be the same as in the non-viviparous *Poa arctica*, *i. e.* $2n = 56$ (Fig. 59). But in this chromosome complement there are four remarkably short, almost fragment-like chromosomes which could not be observed in the non-viviparous *Poa arctica*. In Fig. 59 these chromosomes are marked *G*.

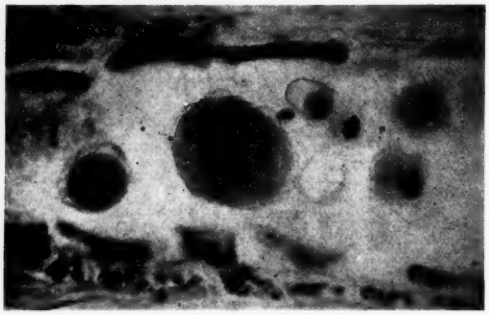
Meiosis was characterized by being most extremely irregular. At metaphase I a larger or smaller number of univalents could almost always be seen scattered about in the plasm and at anaphase I there appeared numerous lagging chromosomes (Fig. 64). The irregularities recur in the second division and at anaphase II the chromosome could



Figs. 64—66. Meiosis in *Poa arctica* v. *vivipara*. — Fig. 64, anaphase I in side view with several lagging chromosomes. — Fig. 65, side view of an anaphase II; the chromosomes scattered in the plasm. — Fig. 66, syndiploid P.M.C., anaphase I with a micronucleus (in side view). Only one plate from the macronucleus (in polar view) is drawn and in this plate 116 chromosomes can be counted. — Magnification: 2700 ×.

often be seen scattered in complete disorder round the entire cell (Fig. 65). Syndiploidy was very common. Fig. 66 shows an anaphase I of a syndiploid pollen mother cell, only one pole being drawn. In this pole 116 chromosomes could be counted. In the same cell is seen an anaphase of a micronucleus in side view. The number of chromosomes

in this cell is four times greater than normal, thus the number has here been doubled and redoubled. The microphotograph, Fig. 67, shows another syndiploid gigas cell. Earlier stages than metaphase I could not be studied, nor was it possible to study the divisions in the sporocytic tissue, consequently the origin of these cells could not be elucidated. It may be mentioned, however, that quite possibly we have here an example of a nucleus transition, »cytomixis» (cf. for instance KIHARA



67

Fig. 67. *Poa arctica* v. *vivipara*. Microphotograph showing a syndiploid P.M.C. in side view of anaphase I, together with P.M.C:s of normal size. — Magnification: 600 ×.

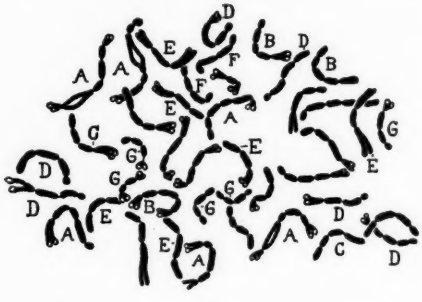
and LILIENFELD, 1934), as sometimes cells devoid of chromatin could be observed lying quite close to syndiploid cells. No real chromatin bridge between the cells was discernible however. Both the syndiploid cells and the majority of the others degenerate shortly before and during the tetrad stage. Only about 3 per cent morphologically good pollen was produced.

23. PUCCINELLIA ANGUSTATA (R. BR.) RAND. ET REDF.

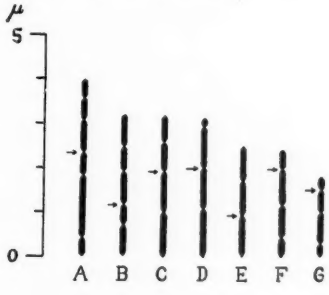
This species is a hexaploid with the chromosome number $2n = 42$ (Fig. 68). The chromosomes are highly segmented, having a relatively large number of secondary constrictions. As the chromosomes, as a rule, were beautifully scattered and regularly extended in the same plane and had also very sharply defined constrictions, a detailed morphological analysis was possible in spite of the somewhat high number. The results of the measurements are recorded in Table 7. In the chromosome complement 7 types of chromosomes could be distinguished, which are reproduced in the diagram of types, Fig. 69. In addition to the diagram of types, examples of each type can be clearly seen in

Fig. 68. Chromosomes of the *D* and *E* types can be seen to the number of six. In other plates the number of chromosomes of other types discernible was six. The morphology of the chromosomes thus points in the direction of autopolyploidy.

In general the course of meiosis is very regular. The metaphase plates are well organised. As a rule only bivalents are seen at diakinesis



68



69

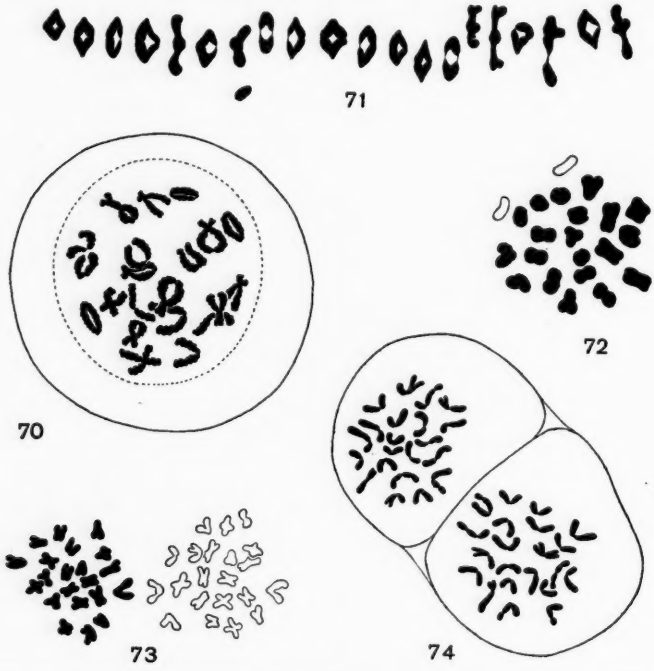
Figs. 68 and 69. *Puccinellia angustata,* 2n = 42. — Fig. 68, somatic metaphase plate; the *D* and *E* types can be seen represented six times. — Magnification: 3600 ×. — Fig. 69, diagrammatic representation of the chromosome types present in the somatic complement. The primary constrictions are indicated by arrows.

(Fig. 70) and at metaphase I. Univalents and trivalents were observed only by way of exception. Fig. 71 shows a metaphase I in side view with the configuration $19_{II} + 1_{I} + 1_{III}$ and Fig. 72 shows a metaphase I in polar view with the configuration $20_{II} + 2_{I}$. Associated groups of a higher order than trivalents were not observed.

TABLE 7. *The average length of the different chromosome types in Puccinellia angustata.*

Type	*A*	*B*	*C*	*D*	*E*	*F*	*G*
Length of the segments in μ	0,4						
	0,5	0,7					
	0,8	0,6	0,6	0,2		0,4	0,3
	0,5	0,7	0,7	0,9	0,8	0,8	0,5
	1,4	0,5	0,9	0,9	0,8	0,8	0,7
	0,4	0,7	1,0	1,1	0,9	0,4	0,3
Total length in μ	4,0	3,2	3,2	3,1	2,5	2,4	1,8

Owing to the fact that univalents and trivalents occur in a few cases an irregular numerical distribution may be expected occasionally. In one case out of 38 anaphase I and metaphase II stages examined the distribution was 20 : 22; the others were normal with the distribution 21 : 21, as shown in Figs. 73 and 74.

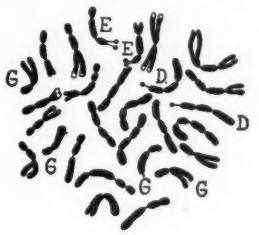


Figs. 70—74. Meiosis in *Puccinellia angustata*. — Fig. 70, diakinesis showing 21 bivalents. — Fig. 71, side view of metaphase I showing $19_{II} + 1_{I} + 1_{III}$, separately drawn. — Fig. 72, polar view of metaphase I with $20_{II} + 2_{I}$. — Fig. 73, polar view of anaphase I, both plates separately drawn, showing the normal segregation (21—21). — Fig. 74, metaphase II with both plates in polar view; 21 chromosomes can be counted in each plate. — Magnification: 2700 ×.

24. PUCCINELLIA PHRYGANODES (TRIN.) SCRIBN. ET MERR.

This essentially sterile species is a tetraploid, $2n = 28$ (Fig. 75). The morphology of the chromosomes indicates that it is an allotetraploid, for its chromosome complement contains two satellite-bearing types, each of which is represented twice. Chromosomes of these two

types, *D* and *E* (v. Fig. 75), differ from each other in their total length — the *D* type chromosomes measure about 2,7 μ and the *E* type chromosomes about 2,1 μ — and moreover the distal segment of the long arm is approximately twice as long in the *D* type chromosomes as in the *E* type. One or two other types seem to be represented four times, for instance the short *G* type. This indicates that the parents of this allopolyploid must have been closely related, since in its broad features their chromosome morphology cannot have differed very much.



75

Fig. 75. Somatic metaphase plate of *Puccinellia phryganodes*, $2n = 28$. Each of the satellite-bearing chromosomes of the *D* and *E* types are seen present only to the number of two, while chromosomes of the *G* type are represented four times. — Magnification: 3600 ×.

Meiosis was found to be very abnormal. At metaphase I the frequency of univalents and multivalents was often high. No case occurred in which only bivalents (14_{II}) were observed. Figs. 76 and 77 show two metaphase I plates in side view with $7_{II} + 3_{I} + 1_{III} + 2_{IV}$ and $6_{II} + 1_{III} + 2_{IV} + 1_{V}$. Conjugated groups of a higher order than quinquevalents were observed and in one case a chain of six and another of twelve chromosomes were observed at pro-metaphase in one and the same cell (Fig. 78). This must therefore be an interchange heterozygote.

At anaphase I and II a larger or smaller number of chromosomes was frequently found to lag (Figs. 79 and 80). No fragments were observed in the somatic chromosome complement, but on the other hand fragmentation was rather common at meiosis. The fragments seem to be eliminated in the plasm. In Fig. 79 a fragment can be seen lying outside the spindle.

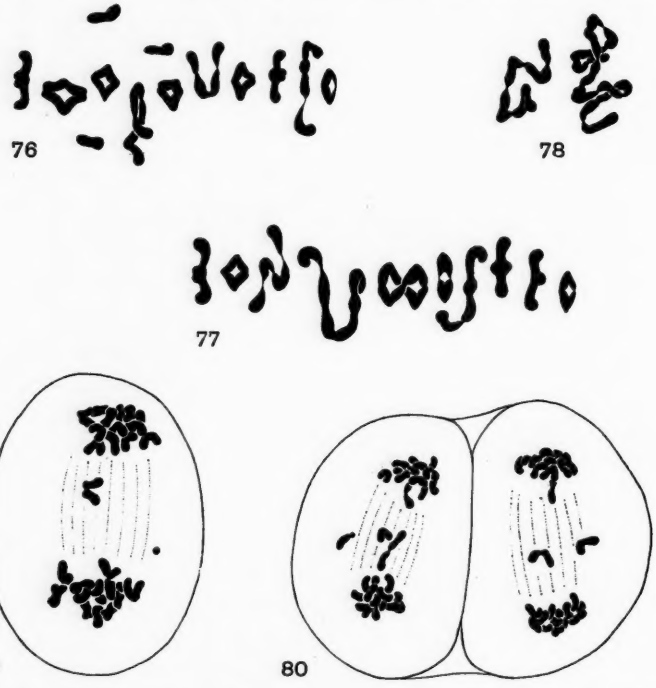
A great many cells appeared to have degenerated in the tetrad stage.

25. PUCCINELLIA VAHLIANA (LIEBM.) SCRIBN. ET MERR.

The somatic chromosome number is 14 (Fig. 81). This is the only diploid species of grass found in Spitsbergen. No other diploids are known in *Puccinellia*, and judging from the literature no diploid has been met with in the closely related genus *Glyceria* from more southern areas.

The chromosome complement in *P. Vahliana* was especially suitable for detailed morphological studies. In general the chromosomes

were beautifully scattered and stretched out in one and the same optic plane. As in *P. angustata,* there also occur here a great many secondary constrictions, which are as a rule very sharply defined. The detailed chromosome morphological data are given in Table 8 and in the diagram of types, Fig. 82. Special mention will be made, however,



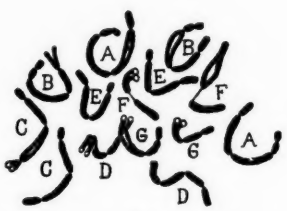
Figs. 76—80. Meiosis in *Puccinellia phryganodes.* — Figs. 76 and 77, side views of metaphase I, separately drawn, showing $7_{II} + 3_{I} + 1_{III} + 2_{IV}$ and $6_{II} + 1_{III} + 2_{IV} + 1v$ respectively. — Fig. 78, two chains, one composed of 6 and the other of 12 chromosomes, both chains from pro-metaphase of a single P.M.C. — Fig. 79, side view of anaphase I with a lagging univalent and a fragment. — Fig. 80, side view of anaphase II with lagging chromosomes. — Magnification: 2700 ×.

of a few types. As appears from Figs. 81 and 82, the chromosomes of the *A* and *B* types are exceedingly alike in respect to the position of both the secondary constrictions and that of the primary constriction. In the metaphase plates they are of the same shape. They are therefore very difficult to differentiate, the only difference between them being a comparatively small difference in length between the long

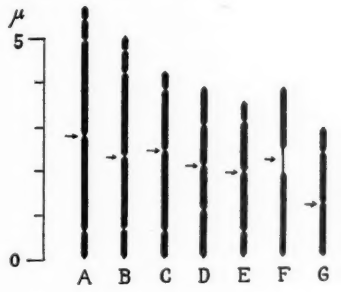
TABLE 8. *The average length of the different chromosome types in Puccinellia Vahliana.*

Type	*A*	*B*	*C*	*D*	*E*	*F*	*G*
Length of the segments in μ	0,3	0,3					
	0,5	0,5	0,4	0,8	0,4		
	2,1	1,9	1,4	0,9	1,2		0,6
	2,1	1,7	1,8	1,0	1,3	1,4	1,1
	0,6	0,6	0,6	1,1	0,6	1,9	1,2
Total length in μ	5,6	5,0	4,2	3,8	3,5	3,3	2,9

proximal segments. As will be seen from Table 8, the distal segments are of exactly the same length in both types. The same thing is true of chromosomes of the *C* and *E* types, even in this case the difference is confined to a certain inequality in the length of the proximal segments.



81



82

Figs. 81 and 82. *Puccinellia Vahliana*, $2n = 14$. — Fig. 81, somatic metaphase plate where the morphology of all the chromosomes can be clearly seen. — Magnification: 3600 ×. — Fig. 82, diagrammatic representation of the chromosome types present in the somatic complement. The primary constrictions are marked by arrows. — Compare the similarity between the *A* and *B* types and between the *C* and *E* types, in respect of their morphological appearance.

In this case we are faced with the same situation as that met with in *Calamagrostis neglecta, viz.* that if the classification into different types is based on other chromosome morphological characteristics than the length of the chromosomes, a classification into 5 types instead of 7 would be more natural.

Of the other chromosomes, mention may be made of those of the *F* type. These chromosomes consist of two relatively long segments

which are separated by a long primary constriction. According to DARLINGTON (1936), the primary constriction is nearly always short. *Aucuba* (MEURMAN, 1929 a), *Aconitum* (DARLINGTON, l. c.) and *Ranunculus* (FLOVIK, 1936) constitute rare exceptions to this rule in that the primary constriction is long in all or nearly all the chromosomes of the complement. In discussing the subject of constrictions DARLINGTON (l. c., p. 39) writes: »The only restriction observable in the free combination of various forms of constriction in different chromosomes is indicated by the rarity of forms with long constrictions separating two limbs of a chromosome. Further, the long constrictions are commonest where the distal element is smallest, *i. e.*, in a trabant, and they are not usually formed in the shortest chromosomes of a complement with a large size range». The state of things in the *F* type chromosomes in *P. Vahliana* must therefore be characterized as exceptional in that the long constriction in these chromosomes is firstly a primary constriction, secondly it has a submedian position and thirdly it occurs in one of the shortest chromosomes of the complement (v. Fig. 81 and Plate I, Fig. 2).

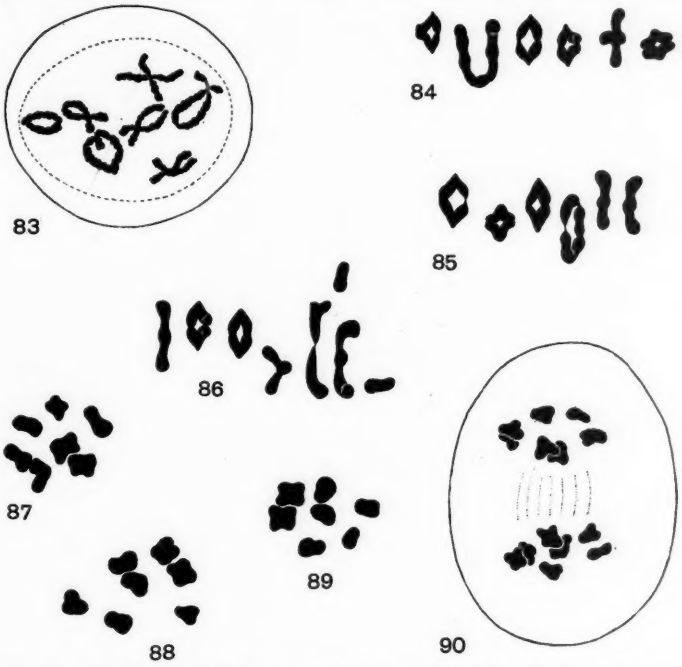
Meiosis runs on the whole a normal course, but certain peculiarities occur in the behaviour of the chromosomes which are of special interest when viewed in connection with the chromosome morphological observations at mitosis.

In 34 cells examined at diakinesis only bivalents were observed, which as a rule were beautifully scattered (Fig. 83). At metaphase I univalents, trivalents and quadrivalents were occasionally observed. But not more than one quadrivalent was observed in any cell. Metaphase plates with $5_{II} + 1_{IV}$ are reproduced in Figs. 84 and 85 (cf. also Plate I, Fig. 5). Fig. 86 shows another metaphase I with $6_{II} + 2_{I}$. Examinations of 70 cells gave the following results:

Configurations	7_{II}	Number of cells	64
»	$5_{II} + 1_{IV}$	» » »	4
»	$5_{II} + 1_{I} + 1_{III}$	» » »	1
»	$6_{II} + 2_{I}$	» » »	1

In polar view of metaphase I secondary associations could be observed very frequently. In this stage of meiosis the chromosomes most frequently appeared in 5 groups (v. Figs. 87, 88 and 89, and Plate I, Fig. 15). The maximum association corresponding to 5 units was observed in 21 out of 38 metaphase plates studied, while of the remaining 17 plates 8 showed secondary associations only between two bi-

valents and in the other 9 the bivalents were spread apart at a uniform distance, as shown in Plate I, Fig. 14. It may be mentioned that for this study cells in which the fixation was good were selected. Further, this secondary association was frequently seen to continue through



Figs. 83—90. Meiosis in *Puccinellia Vahliana*. — Fig. 83, interkinesis; the seven bivalents lying separated from each other. — Figs. 84—86, side views of metaphase I (separately drawn) showing: Figs. 84 and 85, $5_{II} + 1_{IV}$ each, and Fig. 86, $6_{II} + 2_{I}$. — Figs. 87—89, polar views of metaphase I plates with seven bivalents in each. In all the plates secondary association can be seen to occur; two secondary associated groups in each. One group is in all cases composed of the two largest bivalents; the smallest bivalent always being free. — Fig. 90, side view of an anaphase I; seven chromosomes, two of which are secondarily associated, in each pole. — Magnification: 2700 ×.

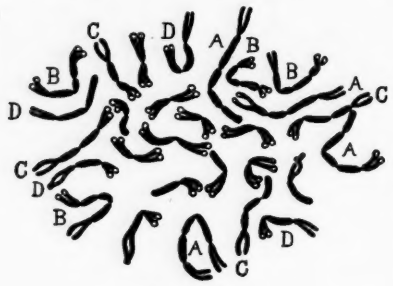
anaphase I (v. Fig. 90). Metaphase II, the stage in which secondary association is often most clearly seen, was however not studied.

An interesting feature is that one of the associated groups always consisted of the two largest bivalents (v. Figs. 87, 88 and 89), which must correspond to the largest and morphologically very similar *A* and *B* chromosome types from mitosis. The smallest bivalent, which prob-

ably corresponds to the *G* type of chromosomes from mitosis, was never seen to participate in any secondary association. The other four bivalents were more equal in size and therefore it was not possible to determine as to what chromosome types the other associated group is composed of.

26. TRISETUM SPICATUM (L.) RICHT.

Trisetum spicatum is a tetraploid with the chromosome number 2n = 28 (Fig. 91). This number was found in the material collected from Spitsbergen as well as in the material from arctic Norway. The limbs of the shortest chromosomes, which were generally orientated close to the centre of the plate, were nearly always more or less bent outside the metaphase plate towards the poles. They had also a strong tendency to be split. In these chromosomes the primary constriction is median or submedian and therefore they are as a rule of the same shape — V-shape; secondary constrictions do not seem to be present. As it was not possible to obtain exact measurements there was no possibility either of separating these chromosomes into different types. The longest chromosomes, which were usually orientated in the periphery of the plate, were on the other hand more suitable for morphological study. Of these chromosomes, those marked *A* and *B* in Fig. 91 constitute an analogy with the *A* and *B* types of chromosomes in *Calamagrostis neglecta* and *Puccinellia Vahliana*, being strikingly alike in every respect with the exception of a certain difference in length — the *A* type chromosomes being on an average 0,8 μ longer than chromosomes of the *B* type. Chromosomes of both these types are made up of five segments. The primary constriction has a submedian position. Each of the two types are represented four times. The next type of chromosomes, type *C*, is easily identifiable, for its representatives consist of four segments, likewise the *D* type, the chromosomes of which are made up of three segments. The two last-mentioned types are again represented four times (v.

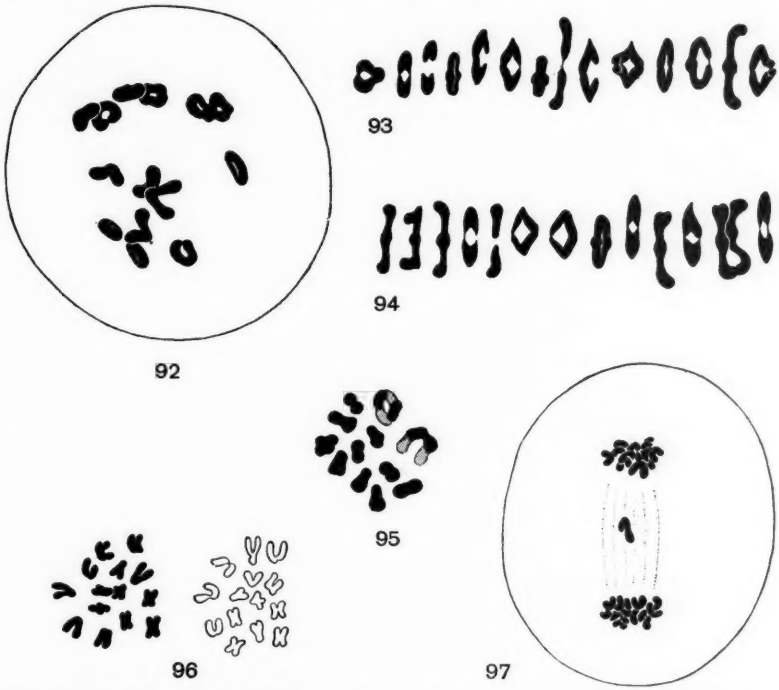


91

Fig. 91. Somatic metaphase plate of *Trisetum spicatum*, 2n = 28. The *A*, *B*, *C* and *D* types can be seen represented four times each. — Magnification: 3600 ×.

Fig. 91). If the morphology of the chromosomes is taken into consideration we are justified in assuming that *Trisetum spicatum* is an autotetraploid.

At pro-metaphase and metaphase I of meiosis univalents, trivalents and quadrivalents were observed in about 50 per cent of the cells exam-



Figs. 92—97. Meiosis in *Trisetum spicatum*. — Fig. 92, pro-metaphase with $12_{II} + 1_{IV}$. — Figs. 93 and 94, side views of metaphase I showing 14_{II} and $12_{II} + 1_{IV}$ respectively. — Fig. 95, polar view of a metaphase I showing $10_{II} + 2_{IV}$. — Fig. 96, polar view of an anaphase I, both the plates separately drawn, showing the normal segregation (14—14). — Fig. 97, side view of an anaphase I with a lagging univalent. — Magnification: 2700 ×.

ined, but not more than two quadrivalents were observed in one and the same cell. Fig. 92 shows a pro-metaphase with $12_{II} + 1_{IV}$. Figs. 93 and 94 from metaphase I in side view show 14_{II} and $12_{II} + 1_{IV}$ respectively, and Fig. 95 representing a metaphase I in polar view shows $10_{II} + 2_{IV}$. In 31 metaphase plates investigated the following configurations were found:

Configurations	14_{II}	Number of cells	16
»	$12_{II} + 1_{IV}$	» » »	8
»	$10_{II} + 2_{IV}$	» » »	4
»	$12_{II} + 1_{III} + 1_{I}$	» » »	1
»	$13_{II} + 2_{I}$	» » »	2

No irregular numerical distribution of chromosomes at anaphase I, which might have been expected in consequence of the non-disjunctional configurations occurring at metaphase I, was met with. The segregation 14 : 14 (Fig. 96) occurred in all anaphase stages examined, 26 in all. Lagging chromosomes at anaphase I (Fig. 97) were observed in only a few cases.

TABLE 9. *List of chromosome numbers (2n) found in Spitsbergen grasses with the name of the locality from which the material was collected.*

Alopecurus alpinus SM., Advent Bay ..... ca. 130 + 1f
» » » , Green Harbour ..... 112 + 3ff, 114 + 2ff
Arctagrostis latifolia (R. BR.) GRISEB., Coles Bay 62
Arctophila fulva (TRIN.) RUPR., Cape Thordsen 42
Calamagrostis neglecta (EHRH.) P. B., Advent Bay 28
Deschampsia alpina ROEM. et SCHULT., Advent Bay 41
» » » » » , Coles Bay 49
» » » » » , Green Harbour ... 39
Dupontia Fisheri R. BR., Advent Bay ..... 88 + 1f, 88 + 3ff
» » » » var. *psilosantha* (RUPR.) SCHOL., Advent Bay ..... 44 + 2ff, 44 + 3ff
Festuca rubra L. var. *arenaria* (OSB.) E. FRIES, Advent Bay 42
» » » » » » » , Green Harbour ..... 42 + 1f
Festuca ovina L. var. *brevifolia* (R. BR.) HART., Advent Bay 28
» » » » *vivipara* L., Advent Bay 49
Hierochloe alpina (LILJEBL.) ROEM. et SCHULT., Advent Bay, Coles Bay 56
Phippsia algida (SOLAND.) R. BR., Advent Bay, Green Harbour 28
Phippsia concinna (TH. FRIES) LINDEB., Advent Bay 28
» » » » var. *algidiformis* (SMITH) HOLMB., Advent Bay 29

Poa abbreviata R. Br., Coles Bay ..... 76 ±
» *alpigena* (E. Fries) Lindm., Advent Bay ..... 84, 77 ±
» » » » var. *colpodea* (Th. Fries) Schol., Advent Bay ..... 51 + 5ff
» *alpigena* (E. Fries) Lindm. var. *vivipara* (Malmgr.) Schol., Green Harbour ..... 42 + 4ff
» *glauca* Vahl, Advent Bay ..... 70—72
» *alpina* L. var. *vivipara* L., Advent Bay ..... 44, 42 + 4ff
» *arctica* R. Br., Advent Bay, Coles Bay, Green Harbour .. 56
» » » » var. *vivipara* (Malmgr.) Schol., Coles Bay 56
Puccinellia angustata (R. Br.) Rand. et Redf., Advent Bay 42
» *phryganodes* (Trin.) Scribn. et Merr., Advent Bay 28
» *Vahliana* (Liebm.) Scribn. et Merr., Advent Bay 14
Trisetum spicatum (L.) Richt., Advent Bay, Coles Bay, Green Harbour 28

IV. DISCUSSION.

1. CHROMOSOME MORPHOLOGY.

Before entering on the real subject of this discussion, namely the primary basic number in grasses, polyploidy in arctic grasses and vivipary in arctic grasses, it may be of interest to mention briefly the morphology of the chromosomes in general.

The theory of permanence, which was first established by Boveri (1887, 1888) and developed by later investigations, was based originally on the generally striking constancy of the chromosome number and the chromosome size. In the light of the results of recent research this theory can be generally said to embrace not only the number and size of the chromosomes but also their shape and constrictions. Objections to the theory of the individuality of the chromosomes and also their genetic continuity, it is true, are not wanting. In his »Kritik der Einwände», Reuter (1930) regards the negative findings with great distrust, and one must agree with his principle, »dass *dunkle, unsichere Fälle im Lichte der klaren und sicheren, der positiv festgestellten Tatsachen beurteilt werden sollten* und nicht umgekehrt» (l. c., p. 180).

Apart from the phylogenetic changes, which Delauney (1926) calls »Historiationen» and »Revolutionen», it may be assumed that the chromosome complement seen in one division is characteristic of the individual and even of the species. »The exceptions to this rule (based on the theory of permanence) are so few that it can be satisfactorily

applied in practice unless there are *a priori* reasons for expecting lack of constancy (as in the examination of mutants or geographical races)» (DARLINGTON, 1936, p. 566).

It is further assumed that differences in the size of the chromosomes of different species will be maintained in their hybrids and derivatives (cf. DARLINGTON, l. c.). This assumption does not always hold good, but the exceptions are provisionally limited to a few unique cases. Exceptional cases of this kind, where the parental chromosomes change in size or length in the hybrid, are certain *Crepis* hybrids (NAVASHIN, 1928, 1934), the hybrid species *Tradescantia brevicaulis* (DARLINGTON, l. c.) and the hybrid *Vicia sativa* × *angustifolia* (SWESCHNIKOWA, 1929 a and b) and a few others. As a rule the alterations in the size or the length of the chromosomes, caused by hybridisation, appear to act in such a way that the chromosomes from one of the parents increase in size or length while those from the other parent decrease. But hybrids are also known in which the change in the chromosomes of both parents is homologous, tending in the direction of a decrease. This is the case in the above-mentioned *Vicia* hybrid (SWESCHNIKOWA, l. c.) and F_2 hybrids of *Dianthus monspessulans* × *D. plumarius* (ROHWEDER, 1934). An analogous instance seems to be provided by the hybrid between *Phippsia algida* and *Ph. concinna* (= *Ph. concinna* var. *algidiformis*) described and examined by the present writer in this paper, in which the chromosomes were found to be considerably shorter (about 20 per cent) and also somewhat slenderer than those in the parents. As already mentioned (p. 307), NAVASHIN (l. c.) has termed changes of this kind »amphiplasty». In his text-book of cytology, DARLINGTON (1932, 1936), in discussing the problem of change of bulk of the chromosomes, assumes that in several cases they are caused by genotypic changes.

Apart from exceptions of the kind mentioned above, cytological, and especially chromosome morphological, characteristics may, in accordance with the generally accepted theory of permanence, furnish very often conclusive evidence. It is on the basis of this theory that chromosome morphological data have been more and more employed in the discussion round systematic and phylogenetic problems, and it is in virtue of the same theory that the chromosome morphological findings have to a great extent been taken as the foundation of most of the conclusions put forward in the present work.

Many different terms have been suggested to denote the structural properties which determine the morphology of the chromosomes (cf.

BRUUN, 1932). The terms most commonly used to denote the three morphologically important characteristics are *primary constriction, secondary constriction* and *satellite* or *trabant* (TAYLOR, 1925, 1926; DARLINGTON, 1926; and BELLING, 1926), and these terms are also used in this work. Instead of primary constriction TAYLOR employs the expression »attachment constriction». In regard to the nature and the cause of these properties opinions may still be said to differ. The main thing in this connection, however, is that they give the chromosomes their individual character so that by their aid, together with other criteria, principally the length of the chromosomes, it is possible to undertake a satisfactory classification of the chromosomes of the complement into different types and to identify these types under different conditions.

As regards grasses there are relatively few publications dealing with the morphology of the chromosomes. From the available works of this kind by various authors it will be seen that secondary constrictions have been observed very rarely or were observed in only a few of the chromosomes of the complement (cf. LEVITSKY, 1929, 1931; MCCLINTOCK, 1929; AVDULOV, 1931; BEADLE, 1932, and others). The secondary constrictions then most frequently observed are of the long type. Contrary to the chromosome morphological studies on grasses carried out by the above-mentioned workers and others — with the exception of RANCKEN's investigations — the present investigation shows that *all species have secondary constrictions in all or mostly all chromosomes* and frequently in an extremely high number, as for instance in *Phippsia* and *Puccinellia.* It is, however, difficult to discover any definite cause or definite conditions which might bring about such a departure from the ordinary with regard to chromosomal structure which these arctic grasses give expression to. Probably the chromosomes in the majority of grass species have a larger or smaller number of secondary constrictions. That they have not been observed is no doubt explained by the fact that the various authors did not have their attention especially directed to these constrictions and also because the majority of them used fixatives which must be considered unsuitable for the preparation of tissues for chromosome morphological studies. Thus different fixatives were tested on several of the grasses dealt with in the present paper and it was found that the contraction and swelling of the chromosomes caused by the poor fixatives affected just the secondary constrictions, which became completely invisible. On the other hand, the primary constrictions were often clearly defined (cf. Fig. 6,

p. 278 from *Arctagrostis latifolia*, where such an unsatisfactory fixative was employed). — In his chromosome morphological studies of grasses, RANCKEN (l. c.), like the present writer, used a fixative containing osmic acid, which has also given very good preparations. A comparison between the chromosome morphological findings in these two investigations is interesting. It will be seen that even in the species examined by RANCKEN there occur numerous secondary constrictions. A noteworthy feature is that *Festuca pratensis* (investigated by RANCKEN) was found to have certain types of chromosomes which are morphologically similar to types found by the present writer in *F. rubra* and *F. ovina*, which is entirely in agreement with the frequently striking similarity of these species in certain external morphological characters and in conformity with the general opinion of their monophyletic origin.

2. THE ORIGINAL BASIC CHROMOSOME NUMBER IN GRASSES.

As is known, there occur a series of different basic numbers in grasses, ranging from 5 to 13. The question has therefore been raised as to whether all these numbers are primary or whether there are among them also secondarily balanced basic numbers. The latter assumption is the more probable. Now since the basic number 7 is the one most frequently occurring, this number is generally assumed to be the true basic number in the family.

AVDULOV (1931) is the only one who has discussed this problem in its widest aspect in relation to the entire *Gramineæ*, and he advanced the hypothesis that the primary basic number is 12. WANSCHER (1934), in discussing the basic chromosome number of the higher plants in common, briefly mentions that the primary basic number in grasses is possibly 8. However, the observations presented in this paper, together with other facts recorded in the literature, give cause for a renewed discussion on the question of the primary basic number in grasses. For there are several reasons for assuming that the originally existing basic number was 5 units. In the following pages these reasons, together with AVDULOV's hypothesis, will be dealt with in detail.

A. EVIDENCE FROM SECONDARY ASSOCIATON OF THE CHROMOSOMES AT MEIOSIS.

DARLINGTON and his school, in particular, have been able to show that there exist two types of pairing or association between chromosomes at meiosis: Primary association with the aid of chiasmata and

secondary association without any material connection. DARLINGTON, in his work on *Prunus* (1928), was the first to distinguish between these two types of association. Later LAWRENCE (1931 a) in a general survey dealt with the problem in detail.

Both types of association refer to conditions of homology. Primary association, which depends on a more intimate, material connection with the aid of chiasmata, exchange of chromatids at the prophase of meiosis, denotes a strong homology. Secondary association, which depends on phylogenetic affinity without any real connection between different chromosomes, usually signifies a somewhat less pronounced homology. This less pronounced homology is thought to be due to a differentiation between originally wholly homologous chromosomes. The cause of the differentiation may be gene mutations or other structural changes (segmental interchange, translocations, deficiencies, etc.), which result in diminishing the affinity to such an extent as to prevent ordinary (primary) pairing or to allow real pairing to take place only in rare cases, as for instance in a hybrid.

The theory has been subjected to a great deal of criticism, especially in connection with the discovery of secondary association in *Pyrus* by DARLINGTON and MOFFETT (1930). The critics, particularly NEBEL (1931, 1933) and SAX (1931), explain the phenomenon essentially as fixation artefacts and usually call it »clumping». As regards *Pyrus*, however, MOFFETT (1931) and recently also HEILBORN (1935) in extensive studies procured evidence which throws the criticism into the shade.

Further, with reference to secondary association MEURMAN (1933) has submitted convincing material from his observations of *Acer platanoides*. The two bivalents which were found to associate at metaphase I could be distinguished by MEURMAN from the other chromosomes both at meiosis and at mitosis, whence this example furnishes an indisputable proof that secondary association is not an accidental occurrence. The haploid chromosome set of 13 units in *Acer platanoides* is thus to be regarded as a secondarily balanced set, derived from an ancestral set of 12 units.

Further references will only be made to the works of MEURMAN (1929 b), LAWRENCE (1929, 1931 b and c), MEURMAN and RANCKEN (1932), MÜNTZING (1933 b), GUSTAFSSON (1934 a and b), NANDI (1936) and NATIVIDADE (1937), and considering the criticism mentioned above it will not be out of place here to cite DARLINGTON himself (1936,

p. 236): »Secondary pairing, like many peculiarities of chromosome behaviour, is exaggerated in appearance by bad fixation, but its essentially differential character as between different chromosomes cannot be determined by an external agent — it is not an artefact».

A hypothesis recently put forward by HEILBORN (1936) may, however, be briefly mentioned. In studying secondary association in *Carex* this author came to the conclusion that chromosomes of equal size are associated irrespective of homology, and he states further (l. c., p. 185) that »it is not a particulate attraction or pairing between homologous parts of chromosomes or homologous genes, but the parallelism of the associated chromosomes is mechanically induced through the polarity of the nuclei». This hypothesis, however, rests on a weak foundation, for it is just in *Carex* we should expect to find secondary pairing in the true meaning of the word, because the chromosome numbers are throughout high and for that reason we may be justified in suspecting the presence of polyploidy in some form or other. The chromosomes in *Carex* are usually very small and consequently the chiasma frequency must be assumed to be low, whence the possible occurrence of polyploidy can hardly make itself evident in prophase pairing to multivalents, but on the other hand in secondary association. The behaviour of the A' and A'' groups of chromosomes in *Carex glauca*, to which HEILBORN attaches great importance in support of his hypothesis, can just as well be taken as evidence that the basic number in this species is secondarily balanced. MÜNTZING (1936) has already considered this idea, for he says (l. c., p. 335): »If the species is a simple autotetraploid the basic number should be 18. Considering that this value is rather high, it is probable that *Carex glauca*, though in the main an autotetraploid species, may have a more complicated constitution and originally a lower basic number». Thus HEILBORN's hypothesis cannot be accepted, at any rate not without further proof, as a weighty argument against DARLINGTON's original interpretation of the phenomenon of secondary association.

In the material available in the present investigation secondary association was observed in *Calamagrostis neglecta* and *Puccinellia Vahliana*. *Calamagrostis neglecta*, however, is a tetraploid ($2n = 28$) and the secondary associated groups observed in this species do not furnish any grounds for conclusions concerning the problem under discussion. *Puccinellia Vahliana*, on the other hand, is a diploid ($2n = 14$) and the frequently occurring secondary association in this species together with the occurrence, although rare, of quadrivalent

formation prove that *there is a homologous relationship between chromosomes within one and the same genome.* This fact together with the results of the chromosome morphological analysis of the somatic chromosome complement therefore constitute a good basis for arriving at more definite conclusions.

The case of *Puccinellia Vahliana* is very clear and fulfils all the criteria for interpreting the associated groups observed as true secondary associations. In the primary, prophase pairing obviously bivalents with but few exceptions are formed. At diakinesis — the stage at which repulsion is strongest — only bivalents were found. In this stage the bivalents lay widely separated. Quadrivalents were, however, certainly observed in side view of metaphase I plates, but as already mentioned, they were very rare (1_{IV} in 4 out of 70 cells examined). In polar view of metaphase I two secondarily associated groups could be frequently observed, each group made up of two bivalents. The maximum association, which thus corresponds to 5 groups of chromosomes at meiosis, was observed in 21 out of 38 metaphase I plates studied. Further, one of the two secondarily associated groups was always seen to consist of the two largest bivalents, that is the *A* and *B* types of chromosomes which were found to be the largest at mitosis and which were approximately morphologically homologous. The smallest bivalent, which corresponds to the *G* type chromosomes from mitosis and was morphologically quite different from the other chromosome types, was never seen to enter into any secondarily associated group. The other four bivalents were more equal in size, consequently it was not possible to decide what chromosome types made up the other associated groups. But it could be observed that the associated bivalents, besides being very much the same in size, were as a rule of the same shape, *i. e.* they were identical in respect to the position and number of the chiasmata and in the position of their primary constrictions.

Further, it may be worth mentioning that in one metaphase plate from mitosis examined the same grouping occurred in one pollen grain as at meiosis, *viz.* two groups, each group consisting of two chromosomes, and three separated chromosomes. In these groups the chromosomes were so close together that in low magnification only 5 units could be differentiated.

In accordance therefore with the assumptions made by different authors in respect to other similar cases of secondary polyploidy in other genera or families, *the haploid chromosome number 7 of Puccin-*

ellia Vahliana should thus be a secondarily balanced set, derived from an ancestral basic set of 5 chromosomes.

In other grasses secondary association has been observed especially in *Oryza sativa* (SAKAI, 1935; NANDI, 1936; cf. also KUWADA, 1910). The present basic number, 12 (v. KUWADA, l. c.; NAKATOMI, 1923 and AVDULOV, 1931), has been shown by SAKAI and especially by NANDI to be a secondarily balanced set derived through secondary polyploidy. Secondary association is a common occurrence and the maximum association corresponding to 5 groups of bivalents and therefore 5 must be regarded as the primary basic number in this species. The same thing is probably true of *Oryza officinalis* (n = 12), in which secondary association also occurs but is not so pronounced as in *O. sativa* (NANDI, l. c.). As regards *O. sativa*, this opinion that 5 is the primary basic number is further supported by chromosome morphological and genetic data (see below).

In *Sorghum*, with the basic number 10, HUSKINS and SMITH (1934) have in several species observed secondary association to be very common but they do not take the matter into further consideration. Still on the basis of other data, which will be mentioned later, these authors come to the conclusion that the basic number of 10 in *Sorghum* is secondarily balanced. LONGLEY (1932) points out that the short-lived annual species, *Sorghum versicolor*, was found to have 5 as its haploid chromosome number, and he therefore assumes that the haploid chromosome number 10 in perennial *Sorghums* represents a duplication of the chromosome set found in annual forms. LONGLEY (l. c., p. 319, Fig. 2 K) has reproduced a drawing of a metaphase II from *S. arundinaceum* (n = 10), in which a beautiful secondary association into 5 groups, each made up of two chromosomes, can be seen. LONGLEY himself, however, does not seem to have noticed this secondary association, which so beautifully supports his opinion that the primary basic number in this species is 5.

Otherwise no positive proof of secondary association is recorded in the literature on the cytology of diploid grass species. This may be thought to be due to the fact that the differentiation has advanced too far. But it is also quite conceivable that the reproduced drawings do not reveal any secondary association because, as LAWRENCE (1931 a, p. 367) points out, »the cytologist always chooses the 'best' plate to draw, *i. e.* the plate which shows the most even distribution of chromosomes in polar view». This of course in order to avoid the suspicion of bad fixation.

B. EVIDENCE FROM THE FORMATION OF QUADRIVALENTS IN DIPLOIDS AND BIVALENTS IN MONO-HAPLOIDS, AND THE UNEXPECTED CONJUGATION IN HYBRIDS.

As already mentioned, a quadrivalent occasionally occurs in addition to the ordinary bivalents in *Puccinellia Vahliana*. A number of similar examples are recorded in the literature, a few of which will be briefly mentioned.

In a careful investigation of *Festuca pratensis*, RANCKEN (1934) found in two individuals a quadrivalent in nearly half the P.M.C:s examined. DARLINGTON (1933) found in *Secale cereale*, in which the pairing was otherwise normal, a group of 8 pollen mother cells, each of which had a quadrivalent ring or chain. In one type of *Dactylis Aschersoniana*, MÜNTZING (1937) found a quadrivalent in about one-third of the examined metaphase I plates. A similar unexpected occurrence of quadrivalents was met with in the hybrid *Triticum ægilopoides baidaricum* × *T. ægilopoides stramineonigrum* (L. SMITH, 1936). All the above-mentioned species are diploids with the basic number 7. In several *Sorghum* species with $n = 10$, HUSKINS and SMITH (1934) found multivalent formation to be relatively common — thus in the same cases as those in which secondary associations were observed (cf. above).

Usually this quadrivalent or multivalent formation is explained by a) segmental interchange, b) translocation or c) translocation with a subsequent reduplication. In the majority of cases in which these conditions are supposed or shown to be the cause of the multivalent formation in other diploid plants, the multivalents usually appear in most of the P.M.C:s of the individual. This is the case in *Datura* (BLAKESLEE, 1928), *Pisum* (HÅKANSSON, 1929, 1931), *Campanula* (GAIRDNER and DARLINGTON, 1930) and several others. In the diploid grasses, on the other hand, this multivalent formation seems to occur only in a few cells. Thus there appears to be a certain difference which indicates that the phenomenon in the diploid grasses is of a somewhat different nature from that occurring in structural hybrids in general.

BURNHAM (1932) with regard to maize, ERLANSON (1933) with regard to *Rosa* and RANCKEN (l. c.) concerning *Festuca*, point out that the more infrequent occurrence of multivalents indicates that the structural changes, when it is a question of translocation or segmental interchange, only involve short chromosomal parts. In conformity with the chiasma theory of chromosome pairing this assumption furnishes a satisfactory explanation of the conditions in a given case. But it

remains an open question why apparently the structural changes in question in grasses should throughout involve smaller chromosomal parts than in other plants. The matter can be just as easily explained, and on the basis of the chiasma theory of chromosome pairing, by the assumption of secondary polyploidy. In this case it is assumed that there are present originally homologous chromosomes between which the differentiation is not more advanced than to allow occasional pairing to take place. In view of the frequent occurrence of secondary association in *Puccinellia*, the differentiation in this case should involve intra-chromosomal rearrangement, for instance inversions or displacement in the sequence of different loci, which may lead to reduced chiasma frequency and consequently a more infrequent occurrence of multivalents.

According to HUSKINS and SMITH (l. c.), the multivalents in *Sorghum* can hardly be due to translocations, for *Sorghum* is predominantly self-fertile and they would therefore be continuously eliminated out of the population. These authors are therefore of opinion that 10 is not the basic number in *Sorghum*, but rather 7, since 7 and multiples of that number are most frequent in grasses. KARPER (1930) and LONGLEY (l. c.), however, found a species, *S. versicolor*, with the haploid set $n = 5$, which number is most probably, as LONGLEY states, the basic number in *Sorghum*.

Another feature, which merits attention in this connection, is the presence of bivalents observed by various investigators in monohaploids. In haploids arisen from diploids, a number of which are known (cf. KATAYAMA, 1935), the chromosomes have normally no homologous partners, and therefore they naturally appear as univalents. There are, however, exceptions to this rule, and it is noteworthy that these exceptions are chiefly met with in the *Gramineæ*. In haploid *Triticum monococcum*, KIHARA and KATAYAMA (1933) and KATAYAMA (l. c.) now and then observed a bivalent. Bivalents have also been observed in haploid *Oryza sativa* (MORINAGA and FUKUSHIMA, 1934), which agrees very well with the view expressed by SAKAI (l. c.) and NANDI (l. c.) that the now existing basic number in *Oryza* is a secondarily balanced basic number. Further, occasional pairing has been observed in haploid pollen grain divisions in polymitotic maize (BEADLE, 1931).

A plausible explanation of this pairing in haploids is no doubt to be found in secondary polyploidy. At any rate attention should be directed as much to the existence of a previous lower basic number as

to translocation or segmental interchange, which phenomena are usually supposed to be the cause.

Secondary polyploidy is also probable in grasses owing to the fact that the unexpected pairing conditions so frequently met with in hybrids between taxonomically widely different species can then be more easily explained as a result of a partial intra-genomatic pairing. On the basis of their observations, BLEIER (1928) and JENKINS (1929) consider it probable that such an autosyndesis between chromosomes belonging to one and the same genome to some extent takes place in hybrids between *Triticum* and *Ægilops*. But this assumption is strongly disputed especially by KIHARA and NISHIYAMA (1930), KIHARA and LILIENFELD (1932) and NISHIYAMA (1934). The view held by BLEIER and JENKINS, which can hardly be said to be unwarranted, will receive renewed force when viewed against the background of the assumption of secondary polyploidy.

C. EVIDENCE FROM CHROMOSOME MORPHOLOGY.

In the description the somatic chromosomes were classified in this paper according to their total length and the different types were denoted with capital letters, generally from *A* to *G* — *A* designating the longest and *G* the shortest chromosome in a given complement. Another, and for this part of the discussion, more suitable classification would be obtained if all morphological characteristics were taken as the foundation, such as segmentation, the relative length of the segments, the position of the primary constriction, etc., that is a classification into basic types. Thus in *Puccinellia Vahliana* chromosomes of the *A* and *B* types are strikingly alike in all respects except for a comparatively slight difference in length (cf. the diagram of types, Fig. 82, p. 323). Therefore if the classification was effected according to the characters mentioned above, the *A* and *B* chromosomes would have to be referred to one and the same type, and if the difference in length is taken into consideration they could appropriately be designated A_1 and A_2. The same thing applies to chromosomes of the *C* and *E* types, and these might very well be denoted with the same letter followed by an index number. The other three types are quite different, as chromosomes belonging to these types are made up of 4, 3 and 2 segments respectively. The number of basic type chromosomes would then be 5, which agrees very closely with the secondary association observed at meiosis, corresponding to 5 groups of chromosomes, and with the assumption of an original basic number of 5 units. The chromosome

complement in *Puccinellia Vahliana* can therefore most appropriately be represented as of the constitution $A_1A_1A_2A_2\ B_1B_1B_2B_2\ CC\ DD\ EE$.

Fully analogous cases to *Puccinellia Vahliana* are *Calamagrostis neglecta*, *Festuca ovina* and, as far as can be judged, *Trisetum spicatum*. In *Calamagrostis neglecta* the *A* and *B* type chromosomes and the *E* and *F* type chromosomes are on the whole morphologically alike. In *Festuca ovina* the similarity is between the *B* and *C* and the *E* and *F* types. In *Trisetum spicatum*, the *A* and *B* types are very similar in appearance and, as far as can be judged, the same thing can be said about two of the shortest types. In all these cases there thus remain only 5 basic types. In a few other species at least two of the types could be combined into one type in the manner described above; thus the *C* and *D* types in *Festuca ovina* var. *brevifolia* and the *F* and *G* types in *Puccinellia angustata*.

With regard to *Festuca pratensis*, RANCKEN (1934) points out that there are two types which are difficult to distinguish from one another.

A similar chromosome morphological analysis of *Oryza sativa*, performed by NANDI (1936), confirmed the result of the observations of secondary association, namely that the primary basic number in that species must be 5.

Such a surprising similarity between two pairs of chromosome types as in *Puccinellia Vahliana*, *Calamagrostris neglecta* and *Festuca ovina*, one cannot obviously expect to find in all cases even if secondary polyploidy is present. Differentiation must of course be assumed to have taken place, and this differentiation will naturally enough also have an effect on the morphology of the chromosomes.

Judging from the chromosome morphological data, the reduplication seems to involve different chromosome types in different cases. If we suppose the original genome to be made up of the types *ABCDE*, the reduplication may in one case involve the *A* and *B* types, in another case the *B* and *C* types, and so on. This partial autopolyploidy must therefore be considered to have been of great evolutionary significance within the family. As appears from the chromosome morphological findings, the chromosomes which are mostly found reduplicated are those belonging to the longest types. That is only natural, as they will form the greatest number of chiasmata and even at metaphase frequently possess interstitial chiasmata, and therefore non-disjunction can more easily take place in the case of these chromosomes than in the case of short chromosomes with more terminalised chiasmata.

D. EVIDENCE FROM GENETIC OBSERVATIONS.

The occurrence of duplicate or polymeric factors may — yet not without certain reservations — be taken as an indication of polyploidy (cf. TJEBBES, 1931; HUSKINS and SMITH, 1934). Regarding diploid *Gramineæ* species with a higher basic number than 5 as secondary polyploids, we should be able to find in these diploids independent groups of polymeric factors. This is also really the case. In maize ($n = 10$), which has undoubtedly been most thoroughly investigated from a genetical point of view, there are, according to the quotations given by HUSKINS and SMITH (l. c.), ten cases of duplicate and three of triplicate genes known. Polymeric factors are also known in *Sorghum* with $n = 10$. These authors therefore state (l. c., p. 392) that »the relative frequency of duplicate factors in maize and *Sorghum* agrees with the cytological evidence that 10 is not their basic chromosome number». Further, in *Oryza sativa* ($n = 12$), in which the basic number must, in conformity with the cytological findings, be considered to be 5 (v. above), there are according to CHAO (1928) not less than 5 groups of polymeric factors known.

Concerning diploid grasses with the basic number 7 the genetic data are still comparatively scanty. But complicated genetic conditions are known to occur and may be taken as evidence of polymery. Here we shall only refer to MATSUURA's »Bibliographical Monograph on Plant Genetics» (MATSUURA, 1929, 1933). An example, which will, however, be mentioned specially, is recorded by WEXELSEN (1934) in barley. In barley the linkage groups I and II possess and show linkage between factors for internode length and early heading. Judging from the data by WEXELSEN and the chromosome maps he furnished, there is a very great difference between linkage groups I and II with respect to the loci of these genes. But that agrees well with the expected intra-chromosomal recombination as an important differentiating factor.

Although the genetic data may be said to be few and do not supply exact proofs, they nevertheless point in a definite direction, that is in the direction of a lower basic number. It cannot be expected either, as LAWRENCE (1931 a) points out, to find in all cases identical genes in the reduplicated chromosomes, because the differentiation may also be assumed to involve the individual genes in such a way that genes which were once identical have differentiated and now govern the same character in different ways. But in genetic experiments there is reason to pay attention to this fact, as *one must expect polymery in diploids as the result of secondary polyploidy.*

E. EVIDENCE FROM THE NOW EXISTING BASIC NUMBERS AND THEIR MULTIPLES.

It has already been mentioned that a series of different basic numbers, from 5 to 13, occurs within the *Gramineæ*. Usually a certain genus or group has the same basic number and forms multiples of this number. The most frequently occurring basic number is 7 and its multiples. According to the lists of chromosome numbers compiled by TISCHLER (1927, 1931, 1936) and others, the chromosome number of more than 300 species is known, of which in round figures three-fourths belong to the 7-series.

The number 5, which is the lowest basic number known within the family, is of special interest, as this number is most naturally to be regarded as the primary number from which the others may be supposed to have arisen in the course of evolution. As already mentioned, representatives from different series can on close investigations be traced back to this lowest basic number known, *viz. Oryza* from the 12-series, *Sorghum* from the 10-series and *Puccinellia, Calamagrostis* and others from the 7-series.

An interesting example is furnished by *Briza. B. minor* occurs with the number $n = 5$, while *B. media* and *B. maxima* have the number $n = 7$. According to AVDULOV (1931), the difference between these species, however, is exceedingly slight and is confined essentially to a difference in size throughout. As is evident from the name, *B. minor*, with the number 5, is the smallest. But this is exactly analogous with the effect generally produced by autopolyploidy. Therefore this should be regarded as a further example of the basic number 7 being secondary to 5 and that 5 is the primary number. AVDULOV, however, maintains, in conformity with his hypothesis (see below), that the number 5 in *B. minor* is derived from the number 7 in the other *Briza* species. It may be mentioned further that KATTERMANN (1933 a) sometimes found a quadrivalent in a few individuals of *B. media*, a fact which can be said to support the assumption that the basic number 7 in this species is secondarily balanced. But as 7 bivalents are the most common and the basic number 7 is the most prevalent in the *Festucinea*, this author considers it improbable that *B. media* is a polymeric mutant of *B. minor* or another similar species having the lower basic number of 5 units.

Phalaris canariensis is an example in which it is possible from the data available to trace an increase of the basic number from 6 to 7. For the diploid form, CHURCH (1929), KATTERMANN (1930) and AVDULOV

(l. c.) give the number n = 6. But for the tetraploid form of the same species NAKAJIMA (1933) gives the number n = 14 — thus having the basic number 7, which is the characteristic basic number of the genus *Phalaris*. The tetraploid form of *Ph. canariensis*, however, is to be regarded of course as secondary to the diploid form and consequently in this case the basic number 7 is secondary to the lower number, n = 6.

In connection with the above-mentioned facts attention may be called to the noteworthy circumstance that polyploid series are much rarer and do not reach the same high degree in genera or groups having high basic numbers as in genera or groups with low basic numbers. This implies no doubt that *diploids with high basic numbers are in reality polyploids*, but in the course of evolution the more conspicuous evidences of polyploidy and thereby the evidences of a lower basic number have been eliminated.

F. THE HYPOTHESIS OF AVDULOV.

The phylogenetic development of all these different basic numbers occurring in grasses has been dealt with especially by AVDULOV (1931). If we accept the hypothesis of a monophyletic origin of the *Gramineæ*, which seems to be the general opinion according to AVDULOV's quotations, and further if we assume that one of the now existing basic numbers corresponds with that of the primitive type, then the others must be regarded as secondarily balanced, derived from the basic number of the primitive type. »Insofern die ausserordentliche Wahrscheinlichkeit des monophyletischen Ursprungs der Familie keinem Zweifel unterliegt, muss die ganze Mannigfaltigkeit der karyotypischen Formen notwendig auf dem Wege der Evolution entstanden sein» (AVDULOV, l. c., p. 418).

On the basis of a number of morphological and anatomical properties, AVDULOV ranks in the first instance the *Bambuseæ*, the *Oryzeæ* and the *Phragmites* as the phylogenetically oldest. That the *Phragmites* especially are of ancient origin is evidenced by palæontological data. Fossil representatives belonging to the *Phragmites* are known from the Middle Tertiary Period and especially from Myocene deposits.

These »oldest» groups are, according to the same author, characterized cytologically by small chromosomes and by having the basic number 12, which is therefore regarded as the primary basic number. The others should then have been derived from these groups by a gradual reduction of the chromosome number passing by 10, 9, 7 to 5,

as for instance in *Anthoxanthum*, which should thus represent the most advanced genus along the lines of evolution.

AVDULOV bases this hypothesis on another hypothesis, namely by assuming that a steady concentration of chromatin has taken place (»Anwachsen der Chromosomen-Dimensionen») and then a subsequent decrease of chromatin by 1) a loss of separate pieces (fragmentation) from one or all of the chromosomes and 2) a loss of entire chromosomes (»Sinken der Grundzahl»).

In the *Bambuseæ*, AVDULOV was, however, unable to determine for certain the chromosome number of any of the species examined, and he therefore gives the numbers approximately from 68 to 74. With regard to the *Oryzeæ*, he bases his conclusions on *Oryza sativa*; but, as already mentioned, the number 12 in this species must, according to the investigations of SAKAI (1935) and NANDI (1936), be secondarily balanced and 5 must be regarded as the original basic number. As to the *Phragmites*, the chromosome numbers are uncertain and it is hardly possible to form a definite opinion concerning the now existing basic number. The widely differing numbers recorded are $2n = 20$, 36, 42, 48 and about 90 (cf. TISCHLER, 1918, 1929, and AVDULOV, l. c.). Thus the very foundation of AVDULOV's hypothesis is exceedingly weak.

As already mentioned, WANSCHER (1934) seems to incline to a similar view, that is a reduction of the basic chromosome number in the *Gramineæ*, for after having pointed out that 7 is the basic number most commonly occurring at present he says (l. c., p. 121): »Whether it (7) takes its origin in the higher number 8 we do not know, the higher fundamental numbers 9 and 10 found at different places of the system and the number 8 itself found in *Secale* species side by side with 7 possibly indicate this higher primitive basic number».

The problem concerning the origin of the 8-chromosomal *Secale* is however, according to LAMM (1936), by no means solved, but LAMM as well as a number of other cytologists who have occupied themselves with the problem are of opinion that the number 8 in this case is secondary to 7 (cf. GOTOH, 1924; STOLZE, 1925; EMME, 1927, 1928; RANDOLPH, 1928; LEVITSKY, 1929, 1931, and DARLINGTON, 1933).

The hypothesis of a general reduction of the basic number from a *primarily* higher number is hardly admissible even from a genetic point of view. In a primary genome, considered as a unit, all chromosomes are obviously assumed to be bearers of vital genes, or at any rate genes characteristic of the family circle. KIHARA and LILIENFELD (1932) give

expression to such a conception of a genome when they say, in connection with the homologous relationship of the genomes (p. 453): »Es enthält aber jedes Genom den gleichen Genbestand, der zugleich das Minimum an Genen darstellt, welches zur normalen Entwicklung und Fortpflanzung unentbehrlich ist». According to these views, a loss of chromosomes from the primary genome would lead to death or give rise to a »life-form» deviating from the family circle.

G. SUMMARIZING REMARKS.

Accepting a monophyletic origin of the family *Gramineæ*, and in conformity with the observations made by the present writer, together with other facts recorded in the literature, there are reasons for assuming that *the original basic number was 5.* Thus *the other, higher basic numbers are to be regarded as secondarily balanced.*

In view of the fact that only a relatively small number of species has been investigated, it may be said that the hypothesis of a primary basic number of 5 units is not yet firmly established, but it has nevertheless some definite facts to support it. Some of these supporting data may also be said to be rather weak, but together they carry a certain conviction in that they all point in the same direction, namely to an originally lower basic number. Briefly the foundation of the hypothesis may be summarized in the following points:

1. *Secondary associations, the maximum number of which corresponds to 5 groups of chromosomes at meiosis, e. g. Puccinellia* and *Oryza.*

2. *Quadrivalent — or multivalent — formation sometimes occurs in diploids*, as for instance in *Dactylis*, *Festuca*, *Briza*, *Secale* and *Sorghum*. *Bivalent formation occurs in mono-haploids, e. g. Triticum* and *Oryza. Unexpected pairing takes place in hybrids between taxonomically widely different species*, which indicates autosyndesis between chromosomes from one and the same genome, for example in hybrids between *Triticum* and *Ægilops*. (These phenomena may also be due to translocation.)

3. *Chromosome morphological analyses show only 5 basic types of chromosomes at mitosis*, for instance in *Calamagrostis*, *Festuca*, *Puccinellia*, *Trisetum* (?) and *Oryza*.

4. *Genetic observations of diploids show that independent groups of polymeric factors are the foundation of certain characters*, as for example in *Hordeum*, *Zea*, *Sorghum* and *Oryza*.

5. *The lowest known basic number within the family is 5, e. g.*

in species of *Briza*, *Anthoxanthum* and *Sorghum*. *Polyploid series are much more frequent in grasses in which the basic number is low than in those having a high basic number, which suggests that diploids with high basic numbers are really polyploids.*

3. THE OCCURRENCE OF POLYPLOIDY IN THE ARCTIC GRASSES.

From Table 9 (p. 328) it will be seen that all grasses from Spitsbergen, with the exception of *Puccinellia Vahliana*, are polyploids. Investigations carried out by HAGERUP (1928, 1931) and TISCHLER (1934) go to show quite definitely that the polyploids are the most suitable forms to withstand climatically unfavourable conditions of growth. Thus it appears that the percentage of polyploids is higher in climatically unfavourable regions than in regions with a more favourable climate. Thus while TISCHLER (l. c.), when studying the flora of Schleswig-Holstein, found that 60 per cent of the species in that province, which have a northern distribution, are polyploids, the corresponding percentage of species characterized by a southern distribution was only 27. Further, TISCHLER calls attention to the interesting fact that while 55 per cent of the examined species from Iceland are polyploids, the corresponding figure for Sicily is only 31 per cent.

Even if the *Gramineæ* are a family which under all circumstances occur with a very high infusion of polyploids, the Spitsbergen grasses constitute an extreme case where, practically speaking, only polyploids are found within a definite area. However, as a more extensive investigation of the chromosome numbers of the Spitsbergen flora will be published later, the problem of polyploidy will be discussed only very briefly in the present work. It may be of interest, however, to mention here that of the 70 species and varieties hitherto examined from this high arctic group of islands, only 14 are diploids, that is, 80 per cent of the species examined are polyploids (the *Cyperaceæ* are not included in this figure). The correlation existing between chromosome number and geographical distribution, demonstrated by TISCHLER, can therefore be convincingly said to stand the test.

The polyploids are usually divided according to their ancestors into two classes: autopolyploids and allopolyploids (cf. KIHARA and ONO, 1926). Representatives of both classes have been repeatedly produced experimentally, and it can be said to be definitely proved that both phenomena, autopolyploidy as well as allopolyploidy, have played a very prominent rôle in evolution. With regard to the significance of autopolyploidy, it is true that there have been differences of

opinion, but, as MÜNTZING (1936) has shown, a far greater evolutionary significance must be ascribed to this form of polyploidy than has generally been supposed. A particularly interesting fact is that when both diploid and polyploid races occur within one and the same species, the polyploid races have as a rule a more alpine or arctic distribution than the diploid. All these cases and the few exceptions known have been treated in detail by MÜNTZING (l. c.) and do not call for any further mention here. An analogous example is found in *Dupontia Fisheri*, which occurs in two different forms. *D. Fisheri* has the chromosome number $2n = 88$ and *D. Fisheri* var. *psilosantha* $2n = 44$. On account of its chromosome morphological characteristics *D. Fisheri* must be considered to have arisen from var. *psilosantha* by a simple chromosome doubling. Although both forms are arctic, there is evidently a difference in their geographical distribution (cf. SCHOLANDER, 1934). The octoploid *D. Fisheri* reaches farther north than the tetraploid var. *psilosantha*. By means of the purely quantitative increase in the number of chromosomes a hardier life-form, more adaptable to high arctic regions, has been produced.

In many cases it is difficult to determine to which class of polyploids the different species of grasses dealt with in this paper are to be referred. If the chromosome morphological characteristics are made the basis of the two denominations, the following species and varieties can, however, be referred to the allopolyploid class: *Arctophila fulva*, *Deschampsia alpina*, *Dupontia Fisheri* and *D. Fisheri* var. *psilosantha*, *Festuca ovina* var. *vivipara*, *Phippsia concinna* var. *algidiformis*, *Poa alpigena* var. *vivipara*, *Poa arctica* var. *vivipara* (?) and *Puccinellia phryganodes*. On the same principle, the following species may be classified among the autopolyploids: *Festuca rubra* var. *arenaria*, *Festuca ovina* var. *brevifolia*, *Phippsia algida*, *Phippsia concinna*, *Puccinellia angustata* and *Trisetum spicatum*. From a chromosome morphological point of view *Calamagrostis neglecta* is a borderline case.

That *Phippsia algida* and *Ph. concinna* are autopolyploids is evidenced, apart from chromosome morphological observations, which show four morphologically homologous genomes, also by the fact that their hybrid, *Ph. concinna* var. *algidiformis*, is quite fertile. As far as *Festuca rubra* var. *arenaria*, *Puccinellia angustata* and *Trisetum spicatum* are concerned, meiosis does not present a typical autopolyploid picture, for in all three of them bivalents predominantly occur. It is a known fact, however, that autopolyploids may behave in the same manner as the three species mentioned, that is, with respect to the

behaviour of the chromosomes at meiosis. In the experimentally produced autopolyploid *Solanum nigrum*, JÖRGENSEN (1928) thus found that bivalents were formed rather regularly. Quadrivalents were less frequently observed. A similar example is furnished by *Fragaria elatior*, which is considered to be an autohexaploid, but in which only bivalents occur at meiosis (LILIENFELD, 1933, 1936). It may therefore be said that while a high frequency of polyvalents at meiosis may most frequently be taken as sure evidence of autopolyploidy, as for instance in *Aucuba japonica* (MEURMAN, 1929 a), *Avena elatior* (KATTERMANN, 1931), *Carex glauca* (HEILBORN, 1932) and *Dactylis glomerata* (MÜNTZING, 1933 c, 1937), to mention only a few, *the absence of multivalents is not an absolute proof of allopolyploidy.*

That *Festuca rubra* is an autopolyploid has also been suggested by FR. NILSSON (1933), for in the hybrid *Festuca rubra* ($n = 21$) $\times$ *Lolium perenne* ($n = 7$) there occurred from 7 to 12 bivalents. FR. NILSSON points out that these bivalents must be due partly to autosyndesis between *F. rubra* chromosomes, which indicates autopolyploidy in that species, and partly to allosyndesis, which points to an intimate family relationship between the two species, *F. rubra* and *L. perenne.*

What is to be regarded as autopolyploidy and what as allopolyploidy is in fact a question concerning which there is at present a great diversity of opinion. The definitions originally given by KIHARA and ONO (l. c.) have been subjected to a rather varying interpretation. DARLINGTON (1928) limits autopolyploidy to refer only to a doubling of the chromosome number in a theoretically pure line, while allopolyploidy is a doubling in a hybrid. LILIENFELD (1936), referring to KIHARA, maintains that homology and not genetic identity is the basis of the classification. When the genomes are not genetically identical, but only homologous, LILIENFELD (l. c.) suggests the term »aniso-autopolyploidy». For the same cases SIMONET (1935) suggests the designation »allopolyploides isochromosomiques». LILIENFELD's representation, however, seems to accord with the opinion most generally held (cf. also MÜNTZING, 1936).

An interesting fact is that arctic grasses (and arctic plants in general) are for the most part dwarfs in spite of the high degree of polyploidy. In the acquirement of this vital character, under the prevalent meagre conditions of growth, polyploidy must be considered to have played a dominant rôle. It is conceivable that the selection of dwarf forms was facilitated by the greater possibilities of variation brought about by polyploidy. DARLINGTON (1936) assumes that the

non-appearance of polyploidy in various plant-groups must be due to the deficient capacity of such species to segregate or mutate to dwarfs. Another possibility of acquiring dwarfiness through polyploidy is found in the circumstance to which STÄHLIN (1929) has called attention, *viz.* that there is an optimum for chromosome increase above which the plant decreases in size. This optimum of a positive correlation between chromosome number and vigour seemed mostly to lie, in the grasses examined by STÄHLIN, between the hexaploid and the octoploid forms. On a further increase of the chromosome number beyond this optimum the cells and at the same time the plant itself began to decrease in size, probably as the result of physiological disturbances, which are thought to be due to the chromatin mass becoming too large in proportion to the plasm content of the cells. This optimum seems to differ greatly in different species. Thus in *Crepis capillaris* (BABCOCK and NAVASHIN, 1930) and *Primula obconica* (SANSOME and PHILP, 1932) the optimum seems to be reached or exceeded already in the tetraploid forms.

A number of other characters of special importance to the arctic plants may also be thought in many cases to have been obtained through polyploidy. There are already many examples known of chromosome increase bringing about considerable physiological changes (cf. MÜNTZING, 1936). Of particular interest in this connection are the observations made by NISHIYAMA on *Avena* (NISHIYAMA, 1934). This author found that in *Avena* there is a positive correlation between chromosome number and resistance to cold. The tetraploid and especially the hexaploid types were found to be the most resistant and the diploid types the least resistant. MÜNTZING's interpretation of this is that quantitative chromosome differences rather than specific genes are responsible for the different degrees of resistance observed.

That the occurrence of polyploidy has played a significant rôle in the formation of the species and forms which have at present their areas of distribution in the arctic regions can hardly be doubted.

4. THE OCCURRENCE OF VIVIPARY IN THE ARCTIC GRASSES.

Vivipary in itself is a problem of considerable biological interest, but in spite of all efforts we know very little about it. The phenomenon of vivipary in grasses has attracted special attention. The classification of the viviparous grasses has always been one of the great taxonomical difficulties and not least within the arctic flora, among which vivipary is especially pronounced. Many systematists have therefore made careful studies of the viviparous form-series, and many highly interest-

ing views have been advanced. Although these studies have brought many important points to light, the problem still remains obscure, because the very essence of the problem — the primary cause of vivipary — has not been given any generally accepted solution, based on reliable observations.

Vivipary includes phenomena of various kinds and according to its nature has been divided, by TURESSON (1926, p. 203), into the following summarizing classes:

»A. *modificatorily* induced as in *Phleum pratense, Dactylis glomerata* and perhaps in most grasses, or

B. *hereditarily* in nature. The grasses of this group may be further divided according to the ecological significance of the vivipary in

a. species, where the genotype factors involved in bringing about vivipary are of no significance ecologically. So apparently in *Zea mays*, and

b. species, where the genotype factors involved in bringing about vivipary have led to the formation of successful habitat races. So in species belonging to the genera *Aira, Festuca* and *Poa*».

Vivipary of TURESSON's Class A was accidentally produced by JENKIN (1922) in *Poa trivialis* and *Deschampsia cæspitosa* by cultivating them under abnormal (greenhouse) conditions. TINCKER (1925) likewise produced vivipary in *Dactylis glomerata* by cultivating it under abnormal conditions of light. In *Cynosurus cristatus*, vivipary seems to occur under abnormal humidity conditions (THOENES, 1929). — EYSTER (1931) was able to identify not less than four genetic factors controlling vivipary in *Zea mays* (TURESSON's Class B. a). But besides being determined by genetic factors the vivipary in maize is strongly influenced in its expression by environmental factors. Vivipary in maize as well as in other plants is regarded by EYSTER (l. c.) as a primitive plant character which, by the interaction of genetic factors and unfavourable growth conditions, may be inhibited. In the case of maize, MANGELSDORF (1926, 1930) does not use the term vivipary, but calls it »premature germination», which is perhaps a more appropriate expression for the cases in which the phenomenon is of the same character as in maize.

Nobody has succeeded in producing hereditarily induced vivipary of TURESSON's Class B. b; it is this class which is of special interest in connection with the present investigation and which affects the well-known hypothesis of ERNST.

In the first place the cytological irregularities occurring during the reduction and tetrad divisions, which in apogamous plants are

frequently so strikingly similar to those met with in typical species-hybrids, form an essential basis of the above-mentioned hypothesis, »Bastardierung als Ursache der Apogamie im Pflanzenreich» (ERNST, 1918).

This hypothesis has been severely criticized, especially by HOLMGREN (1919) and WINKLER (1920), who maintain that even if hybridisation can very well be supposed to be a significant factor in the origin of apogamous forms, and indeed perhaps a necessary condition, there need not necessarily be a causal relationship between these phenomena. But, as pointed out by SCHNARF (1929) and GUSTAFSSON (1935), ERNST has never tried to maintain that hybridisation by itself is sufficient to produce apomixis, he has only asserted that in all carefully examined cases apomixis was associated with so many cytological and genetical disturbances that intense heterozygosity must be a necessary condition.

The hybridisation hypothesis has also been called into question by a number of other investigators on account of the cytological conditions recently discovered in certain apogamous plants. In certain species of *Potentilla*, MÜNTZING (1928, 1931) found pseudogamy in both diploid and polyploid forms, and the presence of multivalents at meiosis in the polyploid forms is taken by this author as evidence of autopolyploidy, which is also supported still further by the existing highly positive correlation between chromosome number and vigour in the species *P. argentea* and *P. Tabernæmontani* (cf. MÜNTZING, 1936). According to BERGMAN (1934), the triploid apomictic *Hieracium umbellatum* is to be regarded as an autopolyploid arisen from the union of one reduced and one unreduced gamete. *Sorbus aria* subsp. *norvegica* is, according to LILJEFORS (1934), probably apomictic. At meiosis quadrivalents occur in a high frequency, for which reason it is assumed to be an autotetraploid, most probably a derivative of diploid *Sorbus aria*. The apomictic biotypes of *Poa serotina* investigated by KIELLANDER (1935) are likewise considered to be autopolyploids, for quadrivalents occurred at meiosis in the tetraploid biotypes and trivalents in the triploid biotypes. The viviparous forms of *Festuca ovina* (TURESSON, 1930, 1931) have also been mostly regarded as autopolyploids and have been employed as examples to demonstrate the untenability of the hybridisation hypothesis.

As will be seen from the present investigation (see below) there is, however, very strong evidence of allopolyploidy in viviparous *Festuca ovina* — thus evidence in favour of the hypothesis of ERNST. Whether all the other apomictics mentioned above are really autopolyploids as

they are supposed to be, is a matter that cannot be said to have been definitely settled. Nor is it absolutely necessary for the validity of the hybridisation hypothesis that only species hybrids are involved, for as GUSTAFSSON (l. c.) says, it is a matter of little importance whether one assumes crossings within or without the systematic species, for the boundaries of »the systematic species» are conventional and theoretically rather arbitrary.

Now whether the hybridisation hypothesis holds good in all cases or not, it can nevertheless be said that it is still of the same immediate practical importance when regarded in its true sense, namely as *a working hypothesis.*

As regards the viviparous arctic *Poæ*, LINDMAN (1923) strictly adheres to the view that they must in general be regarded as hybrids, *i. e.* in the sense of species hybrids. It is essential to point out that LINDMAN arrives at this conclusion from the external morphological characters. Besides being sterile — that is hybrid sterility — they are frequently morphologically intermediate, particularly in their floral, but also in their vegetative parts. He says (l. c., p. 112): »I therefore think it inevitable, on meeting with viviparous arctic *Poæ*, to regard them as cross-breeds; the classification, then, must be an attempt to determine their parents, *i. e.*, the components of the hybrid combination». But LINDMAN also mentions the possibility that such species as *Poa alpina, P. laxa, P. arctica, P. bulbosa, Deschampsia alpina* and *Dactylis glomerata* may be assumed to occur as viviparous species without being hybrids and that an examination may prove such to be sterile from some external damage, *e. g.*, parasitical animals.

LINDMAN's view, like that of ERNST, has been the subject of much discussion and has been severely criticized in some quarters. In his interesting work on the flora of northern Spitsbergen, SCHOLANDER (1934) in particular has taken up the problem for discussion in conjunction with a careful study of his own material and also an examination of the available herbarium material. Generally speaking, SCHOLANDER comes to the conclusion that the viviparous grasses are unmistakably parallel forms of the flowering species. He says (l. c., p. 85): »As far as I can understand, there is no ground for considering viviparity, as a matter of course, as an indicator of hybridity in general. Viviparity is a rather common property in grasses and, to some extent, also in other families, *e. g.* in the *Cyperaceæ*. These viviparous forms occur perhaps in most instances as unmistakably parallel forms of the flowering species, and then frequently in cases where there does not

exist any reason for presuming that viviparity is species hybridogenous» . . . and further as regards the *Poæ*: »As to the question of the cause of viviparity, we cannot in any way draw general conclusions from the facts available — as to whether it is produced by sterility for some reason or other, whether it is a spontaneous (loss?) mutation or what not; and for these reasons the phenomenon of viviparity must be entirely excluded from the discussion as to whether these arctic *Poæ* should be regarded as species hybrids».

In the discussion SCHOLANDER seems, however, to include also facultative vivipary and therefore his opinion that the viviparous grasses are mostly unmistakably parallel forms of the flowering species is understandable. In dealing with the individual species the same author calls attention to a number of interesting and important features, but it should be emphasized that the conclusions are drawn under all reserve, for he rightly says that »taxonomical studies will hardly bring anything else but conjectures in these problems» (l. c., p. 68).

In connection with the different views prevalent concerning this problem the cytological and in particular the chromosome morphological investigations carried out here are of interest.

Three different biotypes of the viviparous species *Deschampsia alpina* were examined, all three biotypes having different chromosome numbers, *viz.* $2n = 49$, 41 and 39. Of these three biotypes the 49-chromosome biotype is especially interesting. Since the basic number in *Deschampsia* must be considered to be 7, we have here a heptaploid, and this odd multiple alone furnishes sufficient reason to assume that the plant is a hybrid, for the number $2n = 49$ cannot normally be supposed to have arisen by a fusion of normal and unreduced gametes from one and the same »karyo-ecotype», to employ MATSUURA's term (MATSUURA, 1935). Nor can it be supposed to have arisen by a simple somatic chromosome doubling, but must of course be interpreted as the result of a crossing between individuals having different chromosome numbers. The study of the morphology of the chromosomes furnishes further confirmation that this biotype is of hybridogenous origin, which is in fact also true of the other two biotypes, having 41 and 39 chromosomes respectively. Most attention was of course devoted to the chromosome complement of the 49-chromosome biotype, because in this case the chromosome number formed a multiple of 7 and can therefore be assumed to possess all the chromosome types characteristic of the species. In this complement only two examples were found of each of the two easily identifiable types *A* and *G*. In the other two biotypes

only two *A* type chromosomes were found present. *In accordance with the chromosome morphological facts the examined biotypes of Deschampsia alpina must therefore be regarded as allopolyploids.* — From the results of the present investigation nothing definite can be said as to how the aneuploid numbers, 41 and 39, have arisen. Nor is it possible to draw any conclusions as to what parent species are involved, but there are reasons to believe that further chromosome morphological investigations of different species of *Deschampsia* will furnish certain evidences which may lead to an elucidation of this problem.

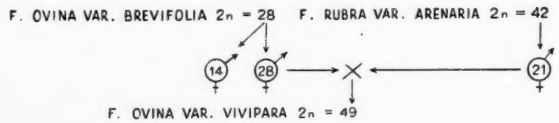
The most interesting case is that of *Festuca ovina* var. *vivipara*. This species has in the past frequently been the subject of discussion, especially as regards its systematic classification and even today there is much disagreement on the subject. DU RIETZ (1926) was of opinion that it must absolutely be regarded as a good species, especially because its geographical distribution differs from that of the common normal *F. ovina*. TURESSON (1926, p. 200), referring to FRIES (1925), points out that its geographical distribution is markedly maritime and »gerade hierin zeigt der vivipare *F. ovina*-Komplex seine Ökotypennatur»; and further: »Will man aber auf Grund der verschiedenen Verbreitung die vivipare *F. ovina* als Art von der übrigen skandinavischen *F. ovina*-Population von obligat sexuellem *vulgaris*-Typus abtrennen, so erscheint mir dies ebenso unberechtigt als wollte man Panzerweizen z. B. von Sveaweizen mit der Motivierung als Art abtrennen, dass erstgenannte Sorte klimatisch an ein ganz anderes Gebiet gebunden ist als letztgenannte». TURESSON (l. c.) divides this viviparous form-complex, as is known, into a number of »formæ apomictæ». SCHOLANDER (cf. DEVOLD and SCHOLANDER, 1933, and SCHOLANDER, 1934) finds it impossible to associate *F. ovina* var. *vivipara* with any form of *F. ovina* or *F. ovina* var. *brevifolia*, and separates it as a distinct species. SCHOLANDER bases his opinion mainly on morphological dissimilarities, especially the differences in the floral parts, and in view of the uncertainty prevailing he employs the neutral and purely morphological name of *F. vivipara*.

Regarding the origin of the viviparous forms, TURESSON (1930), on the basis of the chromosome numbers found, suggests the following possibilities: a) hybridisation between forms having different chromosome numbers or between closely related varieties, as for instance between *F. ovina* var. *vulgaris* and *F. ovina* var. *duriuscula*; b) fertilisation between gametes with unequal numbers of chromosomes from one and

the same parental form; and c) somatic chromosome doubling, which is said to be naturally conceivable chiefly in the case of the high polyploid forms. Thus the author seems to incline mostly to the belief in the occurrence of autopolyploidy, which is also evident from the following sentence (1930, p. 183): »Dass wir es bei diesen Formen am ehesten mit Autopolyploidie zu tun haben und nicht mit Allopolyploidie scheint mir aus dem Umstande hervorzugehen, dass die »Sterilität» mit steigender Chromosomenzahl zunimmt; bei der hexaploiden apm. *tennforsiensis* fehlen ja die Spätsprossinfloreszenzen ganz und gar».

Of the viviparous forms of *F. ovina* examined by the present writer, the 49-chromosome form from Spitsbergen will be mentioned first. As already pointed out with regard to the 49-chromosomal *Deschampsia alpina*, the number $2n = 49$ may be assumed to have arisen by a crossing between individuals with different chromosome numbers. The result of the chromosome morphological analysis indicated that it was of *allopolyploid origin* and that its chromosome complement may be assumed to be made up of four genomes from one of the parent species and three genomes from the other. Comparative morphological investigations of the chromosome complement of *F. ovina* var. *brevifolia*, which at least from a chromosome morphological point of view must be regarded as an autotetraploid, revealed the presence of chromosomes which are morphologically homologous with a few of those found in *F. ovina* var. *vivipara*. The main stress is laid on the characteristic and easily identifiable chromosomes of the *A* and *E* types, of which the *A* type chromosomes were found to be represented four times in *F. ovina* var. *vivipara*. It may therefore be assumed that *F. ovina* var. *brevifolia is one of the parental species of the viviparous form of F. ovina under discussion*. The remaining three *A* type chromosomes in *F. ovina* var. *vivipara* were found on comparison to be morphologically homologous with the *A* type of chromosomes in *F. rubra* var. *arenaria*, and moreover the characteristic *E* type of chromosome of *F. rubra* var. *arenaria* was also found for certain to be represented in the viviparous *F. ovina*.

From the above facts it may be concluded that *Festuca ovina* var. *vivipara from Spitsbergen is a species hybrid arisen from a cross between F. ovina* var. *brevifolia and F. rubra* var. *arenaria*. The chromosome numbers in the parent species and in the hybrid and the numerical proportion in which the individual types of chromosomes are represented, show that *a fertilisation between an unreduced gamete from F. ovina* var. *brevifolia and a normal gamete from F. rubra* var. *arenaria must have taken place*. The following scheme may illustrate the relationship:



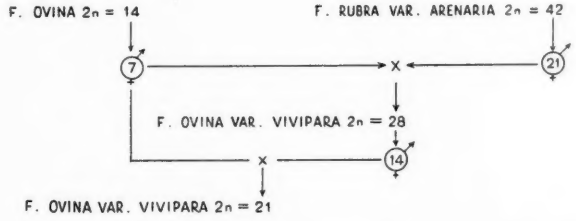
Cytological investigations of viviparous *F. ovina* from arctic Norway gave a similar result as that described above for the viviparous form from Spitsbergen. In normal *F. ovina* the chromosome number was 2n = 14, and in the var. *vivipara* 2n = 28 and 21 for entirely and semi-viviparous forms respectively, *i. e.* the same numbers as those given by TURESSON (1930, 1931) for the forms investigated by him. But while TURESSON (1931) found, in the case of the viviparous forms, that only triploid forms (with the exception of a hexaploid form from the province of Jämtland) occurred on the Scandinavian mainland and tetraploid forms on the islands (Lofoten Islands and the Faroe Islands) and in Scotland, the tetraploid form was found by the present writer to be just as frequent on the mainland as the triploid form, and it was also found in the vicinity of Narvik, where TURESSON collected part of his material. Similarly, triploid and tetraploid forms were found side by side on the islands in the neighbourhood of Tromsö. Thus a well-defined phytogeographical segregation of the viviparous complex of forms into the two 21- and 28- chromosome groups, which TURESSON considers to be a legitimate assumption, does not seem to be the case.

F. rubra var. *arenaria* from the same localities as *F. ovina* and *F. ovina* var. *vivipara* was always found to have the chromosome number 2n = 42. From a chromosome morphological point of view *F. ovina* and *F. rubra* were found to have much in common, but a marked difference could nevertheless be established between the two species with respect to the chromosomes of the *G* type. Thus chromosomes belonging to the *G* type were about 1,4 μ shorter in *F. rubra* var. *arenaria* than in *F. ovina*. Further, the *G* type chromosomes in *F. ovina* have a secondary constriction, which could not be observed in the chromosomes of the corresponding type in *F. rubra* var. *arenaria*.

As regards chromosome number, *F. ovina* var. *vivipara* is fully in accordance with what might be expected in the progeny of an eventual cross between *F. ovina* and *F. rubra* var. *arenaria*. Chromosomes, morphologically homologous with those of the *G* type in *F. rubra* var. *arenaria*, but which were not found in *F. ovina*, were also observed to be present to the number of three. An obvious and natural assumption

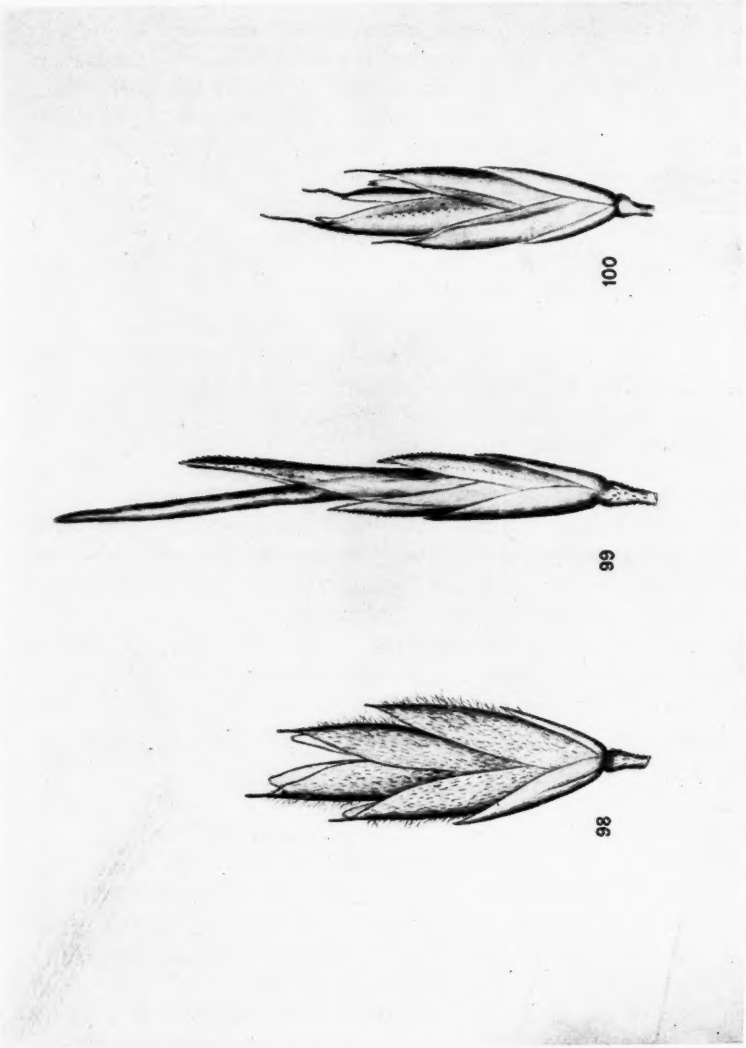
is that *the variety in question is a hybrid between the above-mentioned two species, F. ovina* and *F. rubra* var. *arenaria.*

The material of the semi-viviparous, 21-chromosomal *F. ovina* available for chromosome morphological studies was very limited, on that account it will have to be subjected to a more thorough examination later. Still even in the chromosome complement of this form there seems to occur one or two short chromosomes corresponding to the *G* type chromosomes in *F. rubra* var. *arenaria.* If this is, as appears probable, also a hybrid between the two *Festuca* species, its origin is at present obscure. No *Festuca rubra* form having 28 chromosomes has been found; but such a 21-chromosome form may very easily be supposed to arise by a cross between *F. ovina* ($2n = 14$) and *F. ovina* var. *vivipara* ($2n = 28$). It would thus receive its *F. rubra* chromosomes from the 28-chromosome var. *vivipara*, which sometimes, especially in the later part of the summer, may produce a number of flowers with fully developed and probably even fully functionable sexual organs. The development may therefore be supposed to take place according to the following scheme:



The conclusions drawn on the basis of the cytological data are also supported by other facts which are worth calling attention to. *F. ovina* var. *brevifolia*, whose geographical distribution is mainly arctic, has always glabrous glumas and glumellas (Fig. 100); judging from the literature, no pubescent form seems to exist. The same thing is true of the northern representatives of *F. ovina* (Fig. 104). On the other hand, the representatives of *F. rubra* occurring in the arctic regions are predominantly typically pubescent and are frequently referred to the tomentose var. *arenaria* (Figs. 98 and 101). *F. ovina* var. *vivipara* occurs in the same localities partly glabrous and partly in a pilous parallel form — thus as far as this character is concerned it resembles partly *F. ovina* and *F. ovina* var. *brevifolia* and partly *F. rubra* var. *arenaria.* In Spitsbergen the pilous form is rarer and no

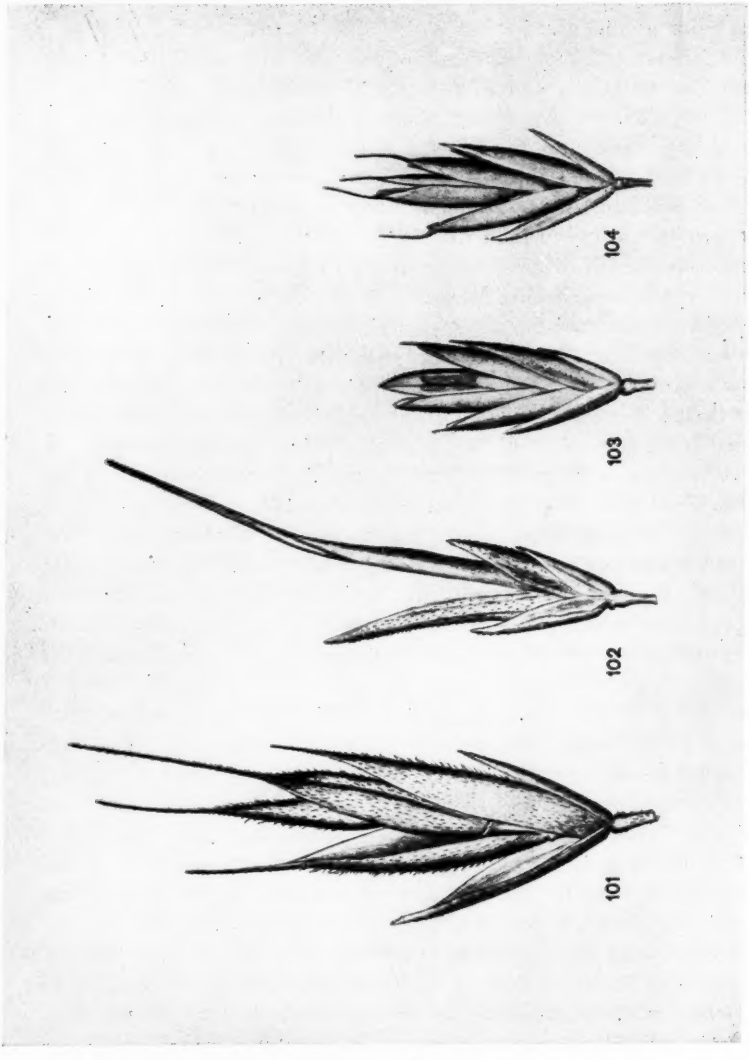
material of this form could be procured for cytological study. The investigated 49-chromosome form from Spitsbergen is glabrous (Fig. 99),



Figs. 98—100. Drawings of spikelets of the different *Festuca* species from Spitsbergen. — Fig. 98, *F. rubra* v. *arenaria*. The glumella is densely hairy. — Fig. 99, *F. ovina* v. *vivipara*. The glumella is glabrous and the awn is lacking. — Fig. 100, *F. ovina* v. *brevifolia*. The glumella is glabrous.

but *F. ovina* var. *brevifolia* contributes the highest number of chromosomes to this form and therefore dominates with respect to the character

in question. The viviparous, 28-chromosome *F. ovina* from arctic Norway was in all the examples examined slightly pubescent, thus if



Figs. 101—104. Drawings of spikelets of different *Festuca* species from arctic Norway. — Fig. 101, *F. rubra* v. *arenaria*. The glumella is hairy. — Fig. 102, *F. ovina* v. *vivipara* (2n = 28) with hairy glumellas and lacking awn. — Fig. 103, semi-viviparous *F. ovina* (2n = 21). The glumella is glabrous and a short awn can be seen. — Fig. 104, *F. ovina* with glabrous glumellas.

anything intermediate between *F. rubra* var. *arenaria* and *F. ovina* (Fig. 102). In this case the greatest number of chromosomes is derived

from *F. rubra* var. *arenaria*, which is therefore dominant for this character. The semi-viviparous, 21-chromosome *F. ovina* may be characterized as glabrous (Fig. 103), but examples were found with slightly hairy glumellas.

The completely viviparous forms of *F. ovina*, in contrast to *F. ovina*, *F. ovina* var. *brevifolia* and *F. rubra* var. *arenaria*, is entirely devoid of awn and palea. In this respect there is a complete analogy between the 49-chromosome and the 28-chromosome forms of var. *vivipara* (Figs. 99 and 102). In the 21-chromosome var. *vivipara* a short awn was rather common, but the shape of it more closely resembles the awn in *F. rubra* var. *arenaria* than that in *F. ovina* (Fig. 103).

There are also other characters which on close inspection argue in favour of the conclusions drawn from the cytological observations. Thus, *F. ovina* var. *vivipara* often resembles very closely *F. rubra* with respect to the colour of the leaves and the culm, the shape of the leaves, etc., and therefore in the opinion of the present writer there can hardly be any doubt that, as is evident from the cytological and other data presented here, *the origin of the allopolyploid, viviparous complex of forms in question is a hybridisation between F. ovina and F. rubra.*

Like *Deschampsia alpina* and *Festuca ovina* var. *vivipara*, *Poa alpigena* var. *vivipara* must also be regarded as an allopolyploid. The chromosome number was found to be $2n = 42 + 4ff$. A characteristic type of chromosome, the *A* type, differing widely from the other types, was represented only twice. Further, chromosomes of the comparatively easily identifiable *G* type were found represented only four times. On account of these chromosome morphological conditions *the chromosome complement of this hexaploid P. alpigena* var. *vivipara is therefore of an allopolyploid character, and must be assumed to be made up of two genomes from one of the parental species and four from the other.* Nothing definite can be said as to what parental species are involved in this case. The cytological data do not furnish any sure clues.

It may be pointed out here that fragmentation seems to be a rather common occurrence in grasses, and particularly in *Poa*. RANCKEN (1934) calls attention to the fact that the aneuploid chromosome number in *Poa* may be assumed to be partly due to fragments, instances of which are also furnished by this investigation. The above-mentioned *P. alpigena* var. *vivipara* constitutes such an example. But the majority of the aneuploid chromosome numbers in *Poa* must, however, be assumed to be due to an irregular numerical distribution during meiosis,

which leads to the formation of gametes having varying chromosome numbers, — cf. MÜNTZING (1933 a) concerning *P. alpina*.

With regard to the extremely arctic and, as a rule, highly viviparous *P. alpigena* var. *colpodea*, the cytological data obtained do not supply any definite evidence of its being of hybrid origin. In the two types examined the chromosome number was $2n = 51 + 5ff$. Its pronounced sterility and the fact that it frequently occurs as an intermediate form between *P. alpigena* and *P. arctica* give strong reasons for assuming that it is of hybrid origin.

In non-viviparous *P. alpigena* the chromosome numbers $2n = 84$ and 77 $\pm$ were found. Thus, of the forms of this species examined, the viviparous forms were found to have much lower chromosome numbers than the non-viviparous forms. As far as can be judged, seed-formation in normal *P. alpigena* is apomictic. In spite of the abnormal course of meiosis, which must necessarily lead to the formation of gametes with exceedingly variable chromosome numbers, the chromosome number in the progeny was found to be constant and the same as that in the mother plant. Besides, the progeny possesses a strict uniformity. That *P. alpigena* has in general apomictic seed-formation is further supported by investigations of this species from arctic Norway, which are at present being carried on in conjunction with practical breeding work, and which will be mentioned here only preliminarily. Four different biotypes from arctic Norway examined so far exhibit the same irregular course of meiosis as those described from Spitsbergen. In the offspring, however, the chromosome number remains constant and in each individual case is the same as in the mother plant. Further, strict uniformity prevails within each biotype in every respect.

Apomictic seed-formation seems to be very common in *Poa*. Thus, in addition to the above-mentioned *P. alpigena*, seed-formation is in all probability apomictic in *P. glauca* and *P. arctica*. Further, apomictic seed-formation has been found to be common in *P. pratensis* (MÜNTZING, 1933 a, 1935 b, and ÅKERBERG, 1936 a and b), in certain biotypes of *P. alpina* (MÜNTZING, l. c.) and in *P. serotina* (KIELLANDER, 1935).

Two biotypes of *Poa alpina* var. *vivipara* from Spitsbergen have been examined. The chromosome numbers of these two biotypes were $2n = 44$ and $2n = 42 + 4ff$. A third biotype from arctic Norway was found to have the number $2n = 33$. From the chromosome numbers alone no definite information can be obtained, however, to elucidate the problem which is of vital and immediate importance here, that is, whether there exists auto- or allopolyploidy. Meiosis in the examined

biotypes, however, conveys a hybridogenous impression, which is indeed the case in all species and varieties of *Poa* examined in this investigation. STÄHLIN (1929) found the same chromosome number (2n = 42) in *P. alpina* var. *vivipara* as in normal non-viviparous *P. alpina*; but this author says (l. c., p. 350): »Die Möglichkeit dass die bulbillentragenden Formen trotzdem Bastarde, eben von zwei Eltern mit gleich viel Chromosomen, sind, bleibt . . . immer noch bestehen».

The extraordinarily great number of forms (cf. TURESSON, 1927) may also be said to point to a hybridogenous origin of *P. alpina* var. *vivipara*. ZOLLIKOFER (1930) points out that the great number of intermediate forms occurring as clones within this series of forms suggests a hybridogenous origin.

In *Poa arctica* var. *vivipara* the chromosome number was found to be the same as in non-viviparous forms of the same species, *viz.* 2n=56. But in the chromosome complement of the var. *vivipara* were found four short chromosomes of a type that could not be ascertained present in non-viviparous *P. arctica*. These four chromosomes were considerably larger than the fragment-chromosomes in the other *Poa* species (*P. alpigena* var. *vivipara*, *P. alpigena* var. *colpodea* and *P. alpina* var. *vivipara*). It is therefore doubtful whether these chromosomes are to be regarded as fragments or as normal chromosomes belonging to the normal complement. In either case the chromosome complement differs from that of normal non-viviparous *P. arctica*, and if these chromosomes are not to be classified as fragments, we have here an allo-octoploid form.

In both cases, in the normal as well as in the viviparous form of *P. arctica*, the course of meiosis was exceedingly irregular, but in this respect var. *vivipara* was the more extreme. A noteworthy feature is the occurrence of syndiploid P.M.C:s in the var. *vivipara*. This phenomenon has been observed in several plants, but what is of interest in this connection is that syndiploidy has been most frequently observed in typical hybrid species. This is the case in *Raphanobrassica* (KARPECHENKO, 1927), in hybrids between *Triticum* and *Ægilops* (KAGAWA, 1929; KATTERMANN, 1932, 1933 b; KIHARA and LILIENFELD, 1934), in several hybrid species in the genus *Chrysanthemum* (SHIMOTOMAI, 1931, 1933) and in the hybrid *Festuca arundinacea* × *F. gigantea* (FR. NILSSON, 1935).

Thus even if it cannot be said to be definitely settled that the viviparous *Poa arctica* in question is of hybrid origin, the cytological data nevertheless strongly point to its hybridity.

As already mentioned, non-viviparous *P. arctica* is in all probability apomictic. But it can be safely assumed that in this species as well as in the other supposed apomictic species of *Poa* there also occur sexually reproducing individuals. In *P. alpina,* MÜNTZING (1933 a) found both sexually reproducing and apomictic biotypes. Absolute apomixis does not prevail either in *P. pratensis.* MÜNTZING (1935 b) mentions that in the apomictic material of this species there appeared spontaneously a sexually reproducing individual. ÅKERBERG (1936 a and b) was able to ascertain that several of the biotypes of *P. pratensis* examined by him were pseudogamous. Pollen from *P. alpina* was found to have much the same effect on seed-formation in *P. pratensis* as pollen from the latter species itself. Usually pollen from *P. alpina* induces only an apomictic seed-formation but occasionally, however, real hybrids arose.

The non-existence of absolute apomixis in the different arctic *Poa* species is also a necessary condition before the morphologically continuous series of forms actually existing between different *Poa* species could have arisen, as, for instance, the series between *P. alpigena* and *P. arctica.*

That not only intermediates occur, but also continuous series, is in conformity with the irregular numerical distribution of the chromosomes to the gametes, which must necessarily occur in consequence of the behaviour of the chromosomes at meiosis. If, for instance, we regard the series *P. alpigena—P. arctica* as a hybrid series, in one case the hybrid may have received the majority of its chromosomes from *P. alpigena* and consequently the predominant number of genes characteristic of that species, and therefore the hybrid will be most closely related to *P. alpigena.* In another case the majority of the chromosomes may be derived from *P. arctica,* in which event it will of course dominate and taxonomically the hybrid must be referred to the same species. This circumstance, together with apomictic seed-formation and viviparity which preserve the new forms, should furnish a satisfactory explanation of the complex phenomenon produced by the arctic *Poæ.*

From the data and views presented concerning the viviparous arctic grasses, it is evident that these forms must *a priori* be regarded as *allopolyploids.* Thus, if the conceptions of ERNST and LINDMAN, previously mentioned, can be said to hold good, the genetical side of the problem, however, is by no means clarified. GUSTAFSSON (1935, p. 63) says on the subject of apomixis in general: »Hybridisation and increase in chromosome number prove that the genes are often of a

complementary nature and that apomixis is therefore a phenomenon determined by several genes».

In *Festuca ovina* var. *vivipara* the increasing degree of vivipary with an increasing degree of polyploidy points to a cumulative effect of polymeric factors. But on the other hand the viviparous forms of *Poa alpigena* were found to have much lower chromosome numbers than the non-viviparous forms, consequently the degree of polyploidy does not always have the same effect.

Even if hybridisation and polyploidy are perhaps severally capable in isolated cases of creating the essential conditions for vivipary, that does not furnish any satisfactory explanation as to why vivipary — and perhaps apomixis in general — is more frequent in the arctic flora than under other conditions. It is obvious to suppose that the extreme external conditions constitute an important factor, and that it is the combined action of the three factors, *hybridisation*, *polyploidy* and *environment*, which determine the origin of the numerous viviparous series of forms in the arctic regions. Hybridisation and polyploidy provide increased possibilities of variation and the extreme environmental conditions brings about an increased frequency of mutation. Viviparous forms can therefore be more readily supposed to arise in the arctic regions than elsewhere. Moreover the viviparous forms, when they have once arisen, have a surer mode of propagation and thereby greater facilities of existence under the extreme climatic conditions than sexually reproducing forms. Natural selection will therefore favour the viviparous forms.

SUMMARY.

1. The present cytological investigation of arctic grasses comprises mainly grasses from Spitsbergen. The chromosome numbers found in these grasses from Spitsbergen are given in Table 9, p. 328.

2. All species examined in this investigation have secondary constrictions in all or most of the chromosomes of the somatic complement. The chromosomes in the species of *Phippsia* and *Puccinellia* in particular have an extremely high number of such constrictions. The reason why secondary constrictions have otherwise been but rarely observed in grasses is thought to be due to the fact that the different authors did not have their attention specially directed to these constrictions, but perhaps mostly to the fact that less suitable fixatives were employed. Thus in the course of this investigation it was observed that the ap-

pearance of the secondary constrictions is much more affected by the composition of the fixative than the primary constrictions.

A complete chromosome morphological analysis was possible in the following species: *Calamagrostis neglecta*, *Festuca rubra* var. *arenaria*, *F. ovina* and *F. ovina* var. *brevifolia*, *Phippsia algida* and *Ph. concinna*, *Puccinellia angustata* and *P. Vahliana*.

3. The original basic chromosome number in the family *Gramineæ* is discussed. On the basis of the observations made in this investigation and other data obtained from the literature, there is reason to assume an originally existing basic number of 5 units. The higher basic numbers now generally occurring must therefore be regarded as secondarily balanced basic numbers; considerable evidence has been adduced by the aid of which representatives of different now existing series of basic numbers can be traced back to a 5-unit series. A summarized survey of the evidence on which the hypothesis of the existence of an originally lower basic chromosome number of 5 units is based will be found on p. 345.

In connection with the above-mentioned hypothesis the hypothesis of an original basic number of 12 units previously advanced by AVDULOV is criticized.

4. Of the investigated 26 species and varieties of grasses from Spitsbergen, only one is a diploid, *viz*. *Puccinellia Vahliana*. Provisionally it is mentioned that of 70 species and varieties of phanerogamous plants examined so far from this high arctic group of islands only 14 are diploids, *i. e.* about 80 per cent of the species examined are polyploids. This confirms very convincingly the well-known conclusions advanced by HAGERUP and TISCHLER that in climatically unfavourable regions a higher percentage of polyploids will be found than in climatically favourable regions.

5. In the genus *Dupontia* the basic chromosome number was found to be 11. In view of the number and morphology of its chromosomes the octoploid *D. Fisheri* ($2n = 88$) is assumed to have arisen from the tetraploid *D. Fisheri* var. *psilosantha* ($2n = 44$) by a simple chromosome doubling.

6. In accordance with the chromosome morphological findings the tetraploid *Phippsia concinna* var. *algidiformis* must be regarded as a hybrid between *Ph. algida* and *Ph. concinna*. Both the last-mentioned species are to be considered as autotetraploids, their chromosome complements being found to consist of four morphologically homologous genomes. The hybrid, *Ph. concinna* var. *algidiformis*, is completely

fertile without any chromosome doubling having taken place, which provides further evidence that both the parental species are auto-polyploids.

7. From the observations made it would seem, in the opinion of the present writer, that the viviparous grasses examined should be regarded as allopolyploids. As regards *Deschampsia alpina*, *Festuca ovina* var. *vivipara* and *Poa alpigena* var. *vivipara* the chromosome morphological facts furnish very strong evidence of their allopolyploid origin.

The results of comparative chromosome morphological studies indicate that the viviparous *Festuca ovina* from Spitsbergen with the chromosome number $2n = 49$ must be assumed to have arisen through a cross between *F. rubra* var. *arenaria* ($2n = 42$) and *F. ovina* var. *brevifolia* ($2n = 28$). The number $2n = 49$ has arisen by fertilisation between a normal gamete from *F. rubra* var. *arenaria* and an unreduced gamete from *F. ovina* var. *brevifolia*. Similarly, the examined 28-chromosome *F. ovina* var. *vivipara* from arctic Norway is to be regarded as having arisen from a cross between *F. rubra* var. *arenaria* ($2n = 42$) and *F. ovina* ($2n = 14$). The origin of the semi-viviparous, 21-chromosome *F. ovina* is more obscure, but the possibility is mentioned that this form may have arisen through a crossing between *F. ovina* ($2n = 14$) and *F. ovina* var. *vivipara* ($2n = 28$).

Certain external morphological characters furnish further support for the assumption that the different forms of *F. ovina* var. *vivipara* are products of a crossing between *F. rubra* and *F. ovina*, as described above.

It is assumed that vivipary is relatively more common in the arctic flora than elsewhere owing to the combined action of the following three factors: hybridisation, polyploidy and extreme external conditions.

8. Of the normal, non-viviparous *Poæ*, the species *P. alpigena*, *P. glauca* and *P. arctica* have apomictic seed-formation. This view is supported by the following observations: Meiosis in all these three species has a very irregular course, which leads to the formation of gametes with varying numbers of chromosomes. In the progeny of the investigated biotypes the chromosome number, however, remains constant and is in each case the same as that of the mother plant, and moreover the progeny was found to possess a strict uniformity.

Holt, Tromsö, November 1937.

EXPLANATION OF PLATE I.

The magnification of the microphotographs reproduced is for Figs. 1—6, 9—10 and 13—15 2000 ×, and for Figs. 7—8 and 11—12 1350 ×.

Fig. 1. Somatic metaphase plate of *Festuca ovina*, 2n = 14. The two *D* type chromosomes with a long secondary constriction are visible at 6 o'clock and at 9 o'clock.

Fig. 2. Somatic metaphase plate of *Puccinellia Vahliana*, 2n = 14. The two chromosomes of type *F*, with a long primary constriction, can be seen at 12 o'clock.

Fig. 3. Somatic metaphase plate of *Phippsia algida*, 2n = 28.

Fig. 4. Side view of metaphase I of *Calamagrostis neglecta*, showing a quadrivalent — the same as in text-fig. 11.

Fig. 5. Side view of metaphase I of *Puccinellia Vahliana*, showing a quadrivalent — the same as in text-fig. 84.

Fig. 6. Side view of metaphase I of *Calamagrostis neglecta*, showing a univalent and a trivalent (to the left) — from the same P.M.C. as Fig. 4 and text-fig. 11.

Fig. 7. Metaphase II of *Deschampsia alpina*; the micronuclei are forming their own spindles — the same as in text-fig. 21.

Fig. 8. Side view of a late anaphase II of *Festuca ovina* v. *arenaria*, showing a lagging chromosome.

Fig. 9. Polar view of metaphase I of *Calamagrostis neglecta*, showing secondary pairing, four groups of two and six single bivalents.

Fig. 10. Polar view of metaphase II of *Calamagrostis neglecta*, 14 chromosomes can be counted in each plate, some of the chromosomes show secondary pairing.

Fig. 11. Side view of metaphase I of *Poa alpigena* v. *vivipara* with univalents lying outside the plate.

Fig. 12. Side view of anaphase I of *Poa glauca*, with lagging univalents.

Fig. 13. Side views of anaphase I of *Poa arctica*; the lagging univalents are dividing.

Figs. 14—15. Polar views of metaphase I of *Puccinellia Vahliana*. In Fig. 14 the seven bivalents are lying apart; in Fig. 15 secondary association is seen to occur — two groups of two and three solitary bivalents can be counted — the same plate as in text-fig. 87.

LITERATURE CITED.

1. Avdulov, N. P. 1928. Die systematische Karyologie der Familie *Gramineæ*. — Tagebuch des Bot. Kongr. der U.S.S.R., Leningrad. (Cited from Avdulov, 1931.)
2. — 1930. Karyo-systematische Untersuchungen über die Gramineen. — Rep. of Proceed., Fifth intern. Bot. Congr., Cambridge, pp. 247—248.
3. — 1931. Karyo-systematische Untersuchungen der Familie Gramineen. — Bull. of Appl. Bot., Genet. and Plant-Breeding 44, pp. 1—428.
4. — 1933. Ergänzende karyologische Daten zur Systematik der Graminaceen. — Bull. of Appl. Bot., Genet. and Plant-Breeding, Ser. II, 2, pp. 131—134.

5. Babcock, E. B. and Cameron, D. R. 1934. Chromosomes and phylogeny in *Crepis*. — Univ. Calif. Publ. Agri. Sci. 6, pp. 287—324.
6. Babcock, E. B. and Navashin, M. 1930. The genus *Crepis*. — Bibliogr. Genetica 6, pp. 1—90.
7. Beadle, G. W. 1931. A gene in maize for supernumerary cell divisions following meiosis. — Cornell Univ. Agri. Exp. Stat., Mem. 135, pp. 1—12.
8. — 1932. Studies of *Euchlæna* and its hybrids with *Zea mays*. I. Chromosome behaviour in *Euchlæna mexicana* and its hybrids with *Zea mays*. — Zeitschr. f. indukt. Abstamm.- und Vererb.-Lehre 62, pp. 291—304.
9. Belling, J. 1926. The structure of chromosomes. — Brit. Journ. of Exp. Biol. 3, pp. 145—147.
10. Bergman, B. 1934. Zytologische Studien über sexuelles und asexuelles *Hieracium umbellatum*. — Hereditas XX, pp. 47—64.
11. Blakeslee, A. F. 1928. Genetics of *Datura*. — Verh. der V. intern. Kongr. f. Vererb.-Wissensch. Zeitschr. f. indukt. Abstamm.- und Vererb.-Lehre, Suppl.-Band 1, pp. 117—130.
12. Bleier, H. 1928. Zytologische Untersuchungen an seltenen Getreide- und Rübenbastarden. — Verh. der V. intern. Kongr. f. Vererb.-Wissensch. Zeitschr. f. indukt. Abstamm.- und Vererb.-Lehre, Suppl.-Band 1, pp. 447—452.
13. Boveri, T. 1887. Über die Befruchtung der Eier von *Ascaris megalocephala*. — Sitz.-Ber. der Gesellsch. f. Morphol. und Physiol., München 3, pp. 71—80.
14. — 1888. Zellenstudien. II. Die Befruchtung und Teilung des Eies von *Ascaris megalocephala*. — Jena Zeitschr. 22, pp. 685—882.
15. Bruun, H. G. 1932. Cytological studies in *Primula*. — Symbolæ Botanicæ Upsalienses 1, pp. 1—239.
16. Burnham, C. R. 1932. An interchange in maize giving low sterility and chain configurations. — Proceed. Nat. Acad. Sci. 18, pp. 434—440.
17. Chao, L. F. 1928. Linkage studies in rice. — Genetics 13, pp. 133—169.
18. Church, G. L. 1929. Meiotic phenomena in certain *Gramineæ*. I. — Bot. Gazette 87, pp. 608—629.
19. Darlington, C. D. 1926. Chromosome studies in the *Scilleæ*. — Journ. of Genetics 16, pp. 237—251.
20. — 1928. Studies in *Prunus*. I and II. — Journ. of Genetics 19, pp. 213—256.
21. — 1932. Recent advances in cytology. — London.
22. — 1933. The origin and behaviour of chiasmata. VIII. *Secale cereale* (n, 8). — Cytologia 4, pp. 444—452.
23. — 1936. Recent advances in cytology. 2nd ed. — London.
24. Darlington, C. D. and Moffett, A. A. 1930. Primary and secondary chromosome balance in *Pyrus*. — Journ. of Genetics 22, pp. 129—151.
25. Delaunay, L. N. 1926. Phylogenetische Chromosomenverkürzung. — Zeitschr. f. Zellforsch. und mikr. Anat. 4, pp. 338—364.
26. Devold, J. and Scholander, P. F. 1933. Flowering plants and ferns of Southeast Greenland. — Skrifter om Svalbard og Ishavet 56, pp. 1—209. Oslo.
27. Du Rietz, G. E. 1926. Bidrag till Kebnekaiseområdets flora. — Svensk Bot. Tidskr. 20, pp. 43—51.

28. EMME, H. 1927. Zur Cytologie der Gattung *Secale*. — Bull. of Appl. Bot., Genet. and Plant-Breeding 17, pp. 73—100.
29. — 1928. Karyologie der Gattung *Secale* L. — Zeitschr. f. indukt. Abstamm.- und Vererb.-Lehre 47, pp. 99—124.
30. ERLANSON, E. W. 1933. Chromosome pairing, structural hybridity, and fragments in *Rosa*. — Bot. Gazette 94, pp. 551—566.
31. ERNST, A. 1918. Bastardierung als Ursache der Apogamie im Pflanzenreich. — Jena.
32. EYSTER, W. H. 1931. Vivipary in maize. — Genetics 16, pp. 574—590.
33. FAGERLIND, F. 1934. Beiträge zur Kenntnis der Zytologie der Rubiaceen. — Hereditas XIX, pp. 223—232.
34. FLOVIK, K. 1936. The somatic chromosomes of certain arctic species of the genus *Ranunculus*. — Soc. Sci. Fenn., Comm. Biol. V. 7, pp. 1—18.
35. FRIES, TH. C. E. 1925. Die Rolle des Gesteingrundes bei Verbreitung der Gebirgspflanzen in Skandinavien. — Svenska Växtsociol. Sällsk. Handl. 6, Uppsala. (Cited from TURESSON, 1926.)
36. GAIRDNER, A. E. and DARLINGTON, C. D. 1930. Structural variation in the chromosomes of *Campanula persicifolia*. — Nature 125, pp. 87—88.
37. GELEI, J. 1921. Weitere Studien über die Oogenese des *Dendrocoelum lacteum*. II. Die Langskonjugation der Chromosomen. — Archiv f. Zellforsch. 16, pp. 88—169.
38. GOTOH, K. 1924. Über die Chromosomenzahl von *Secale cereale* L. — Bot. Magazine, Tokyo, 38, pp. 135—152.
39. GUSTAFSSON, Å. 1934 a. Primary and secondary association in *Taraxacum*. — Hereditas XX, pp. 1—31.
40. — 1934 b. Secondary association between homologous univalents. — Svensk Bot. Tidskr. 28, pp. 445—460.
41. — 1935. Studies on the mechanism of partbenogenesis. — Hereditas XXI, pp. 1—112.
42. HAGERUP, O. 1928. Morphological and cytological studies of *Bicornes*. — Dansk Bot. Arkiv 6, pp. 1—26.
43. — 1931. Über Polyploidie in Beziehung zu Klima, Ökologie und Phylogenie. — Hereditas XVI, pp. 19—40.
44. HASEGAWA, N. 1932. Comparison of chromosome types in *Disporum*. — Cytologia 3, pp. 350—368.
45. HEILBORN, O. 1924. Chromosome numbers and dimensions, species-formation and phylogeny in the genus *Carex*. — Hereditas V, pp. 129—216.
46. — 1932. Aneuploidy and polyploidy in *Carex*. — Svensk Bot. Tidskr. 26, pp. 137—146.
47. — 1935. Reduction division, pollen lethality and polyploidy in apples. — Acta Horti Bergiani 11, pp. 129—184.
48. — 1936. The mechanics of so-called secondary association between chromosomes. — Hereditas XXII, pp. 167—188.
49. HOLLINGSHEAD, L. and BABCOCK, E. B. 1930. Chromosomes and phylogeny in *Crepis*. — Univ. Calif. Publ. Agri. Sci. 6, pp. 1—53.
50. HOLMBERG, O. R. 1924. Die Gattung *Phippsia* und ihre Arten — Bot. Notiser 1924, pp. 126—134.

51. HOLMBERG, O. R. 1926. Skandinaviens Flora, H. 2. — Stockholm.
52. HOLMGREN, I. 1919. Zytologische Studien über die Fortpflanzung bei den Gattungen *Erigeron* und *Eupatorium*. — Kungl. Svenska Vetenskapsakad. Handl. 59, No. 7, pp. 1—118.
53. HUSKINS, C. L. and SMITH, S. G. 1932. A cytological study of the genus *Sorghum* PERS. I. The somatic chromosomes. — Journ. of Genetics 25, pp. 241—249.
54. — 1934. A cytological study of the genus *Sorghum* PERS. II. The meiotic chromosomes. — Journ. of Genetics 28, pp. 387—395.
55. HÅKANSSON, A. 1929. Chromosomenringe in *Pisum* und ihre mutmassliche genetische Bedeutung. — Hereditas XII, pp. 1—10.
56. — 1931. Über Chromosomenverkettung in *Pisum*. — Hereditas XV, pp. 17—61.
57. JENKIN, T. J. 1922. Notes on vivipary in *Festuca ovina*. — The Bot. Soc. and Exchange Club of the British Isles, VI, 3.
58. — 1933. Interspecific and intergeneric hybrids in herbage grasses. Initial crosses. — Journ. of Genetics 28, pp. 205—264.
59. JENKINS, J. A. 1929. Chromosome homologies in wheat and *Ægilops*. — Amer. Journ. of Bot. 16, pp. 238—245.
60. JÖRGENSEN, C. A. 1928. The experimental formation of heteroploid plants in the genus *Solanum*. — Journ. of Genetics 19, pp. 133—211.
61. KAGAWA, F. 1927. Cytological studies on *Triticum* and *Ægilops*. I. Size and shape of somatic chromosomes. — La Cellule 37, pp. 229—323.
62. — 1929. On the phylogeny of some cereals and related plants as considered from the size and shape of chromosomes. — Japan. Journ. of Bot. 4, pp. 363—383.
63. KARPECHENKO, G. D. 1927. The production of polyploid gametes in hybrids. — Hereditas IX, pp. 349—368.
64. KARPER, R. E. 1930. Inheritance in grain sorghums. — Texas Agri. Exp. Stat. Forty-third Ann. Rep., pp. 48—51
65. KATAYAMA, Y. 1935. Karyological comparisons of haploid plants from octoploid *Ægilotricum* and diploid wheat. — Japan. Journ. of Bot. 7, pp. 349—380.
66. KATTERMANN, G. 1930. Chromosomenuntersuchungen bei Gramineen. — Planta 12, pp. 19—37.
67. — 1931. Über die Bildung polyvalenter Chromosomenverbände bei einigen Gramineen. — Planta 12, pp. 732—774.
68. — 1932. Genetische Beobachtungen und zytologische Untersuchungen an der Nachkommenschaft einer Gattungskreuzung. Teil II. Zytologische Untersuchungen. — Zeitschr. f. indukt. Abstamm.- und Vererb.-Lehre 60, pp. 395—466.
69. — 1933 a. Weitere zytologische Untersuchungen an *Briza media* mit besonderer Berücksichtigung der durch Verbände aus vier Chromosomen ausgezeichneten Pflanzen. — Jahrb. f. wissensch. Bot. 78, pp. 43—91.
70. — 1933 b. Ein Beitrag zur Frage der Dualität der Bestandteile des Bastardkernes. — Planta 18, pp. 751—785.

71. KIELLANDER, C. L. 1935. Apomixis bei *Poa serotina*. — Bot. Notiser 1935, pp. 87—95.

72. KIHARA, H. 1930. Genomanalyse bei *Triticum* und *Ægilops*. I. — KIHARA, H. und NISHIYAMA, I.: Genomaffinitäten in tri-, tetra- und pentaploiden Weizenbastarden. — Cytologia 1, pp. 263—284.

73. — 1932. Genomanalyse bei *Triticum* und *Ægilops*. IV. — KIHARA, H. und LILIENFELD, F.: Untersuchungen an *Ægilops* × *Triticum*- und *Ægilops* × *Ægilops*-Bastarden. — Cytologia 3, pp. 384—456.

74. KIHARA, H. und KATAYAMA, Y. 1933. Reifungsteilungen bei den haploiden *Triticum monococcum*. — Agriculture and Horticulture 8, No. 12, pp. 1—17.

75. KIHARA, H. und LILIENFELD, F. 1934. Kerneinwanderung und Bildung syndiploider Pollen-Mutterzellen bei dem F_1-Bastard *Triticum ægilopoides* × *Ægilops squarrosa*. — Japan. Journ. of Genetics 10, pp. 1—28.

76. KIHARA, H. und ONO, T. 1926. Chromosomenzahlen und systematische Gruppierung der *Rumex*-Arten. — Zeitschr. f. Zellforsch. und mikr. Anat. 4, pp. 475—481.

77. KUWADA, Y. 1910. A cytological study of *Oryza sativa* L. — Bot. Magazine, Tokyo, 24, pp. 267—281.

78. LA COUR, L. 1931. Improvements in everyday technique in plant cytology. — Journ. Roy. Microsc. Soc. 51, pp. 119—126.

79. LAMM, R. 1936. Cytological studies on inbred rye. — Hereditas XXII, pp. 217—240.

80. LANGLET, O. 1932. Über Chromosomenverhältnisse und Systematik der *Ranunculaceæ*. — Svensk Bot. Tidskr. 26, pp. 381—400.

81. LAWRENCE, W. J. C. 1929. The genetics and cytology of *Dahlia* species. — Journ. of Genetics 21, pp. 125—158.

82. — 1931 a. The secondary association of chromosomes. — Cytologia 2, pp. 352—384.

83. — 1931 b. The genetics and cytology of *Dahlia variabilis*. — Journ. of Genetics 24, pp. 257—306.

84. — 1931 c. The chromosome constitution of *Cardamine pratensis* and *Verbascum phœniceum*. — Genetica 13, pp. 183—208.

85. LEVITSKY, G. A. 1928. Zur systematischen Karyologie der Gattung *Festuca*. — Zeitschr. f. indukt. Abstamm.- und Vererb.-Lehre, Suppl.-Band 2, p. 1006.

86. — 1929. Investigation on the morphology of chromosomes. — Proceed. U.S.S.R. Congr. of Genet., Plant- and Animal-Breeding, Leningrad, 2, pp. 87—105.

87. — 1931. The morphology of chromosomes. — Bull. of Appl. Bot., Genet. and Plant-Breeding 27, pp. 19—174.

88. — 1934. New fixing mixtures revealing the morphology of chromosomes. — Compt. Rend. de l'Acad. des Sci. de l'U.S.S.R. 4, pp. 143—145.

89. LEVITSKY, G. A. and KUZMINA, N. E. 1927. Karyological investigations on the systematics and phylogenetics of the genus *Festuca*. — Bull. of Appl. Bot., Genet. and Plant-Breeding 17, pp. 3—37.

90. LILIENFELD, F. A. 1933. Karyologische und genetische Studien an *Fragaria*. Ein tetraploider fertiler Bastard zwischen *F. nipponica* ($n = 7$) und *F. elatior* ($n = 21$). — Japan. Journ. of Bot. 6, pp. 425—458.

91. LILIENFELD, F. A. 1936. Karyologische und genetische Studien an *Fragaria*. II. Ist *Fragaria elatior* eine autopolyploide Pflanze? — Japan. Journ. of Bot. 8, pp. 119—149.
92. LILJEFORS, A. 1934. Über normale und apospore Embryosackentwicklung in der Gattung *Sorbus*, nebst einigen Bemerkungen über die Chromosomenzahlen. — Svensk Bot. Tidskr. 28, pp. 290—299.
93. LINDMAN, C. A. M. 1923. *Poa*. — In LYNGE, B. 1923, pp. 111—125.
94. — 1926. Svensk Fanerogamflora. 2nd ed. — Stockholm.
95. LITARDIÈRE, R. DE. 1923. Sur l'insertion fusoriale des chromosomes somatiques. — Bull. Soc. Bot. France 70, pp. 193—197.
96. LONGLEY, A. E. 1932. Chromosomes in grass *Sorghums*. — Journ. of Agr. Research 44, pp. 317—321.
97. LYNGE, B. 1923. Vascular plants from Novaya-Zemlya. — Rep. of the Scientific Results of the Norwegian Expedition to Novaya-Zemlya 1921. No. 13, pp. 1—151. Kristiania.
98. MANGELSDORF, P. C. 1926. The genetics and morphology of some endosperm characters in maize. — Connecticut Exp. Stat., Bull. 279, pp. 513—614.
99. — 1930. The inheritance of dormancy and premature germination in maize. — Genetics 16, pp. 462—494.
100. MATSUURA, H. 1929. A bibliographical monograph on plant genetics. — Tokyo.
101. — 1933. A bibliographical monograph on plant genetics. — Sapporo.
102. — 1935. On karyo-ecotypes of *Fritillaria camschatcensis* L. — Journ. of the Faculty of Science, Hokkaido Imp. Univ., Ser. V., 3, pp. 219—232.
103. MCCLINTOCK, B. 1929. Chromosome morphology in *Zea mays*. — Science 69, p. 629.
104. MCCULLAGH, D. 1934. Chromosome and chromosome morphology in *Plantaginaceæ*. I. — Genetica 16, pp. 1—44.
105. MEURMAN, O. 1929 a. Association and types of chromosomes in *Aucuba japonica*. — Hereditas XII, pp. 179—209.
106. — 1929 b. *Prunus laurocerasus* L., a species showing high polyploidy. — Journ. of Genetics 21, pp. 85—94.
107. — 1933. Chromosome morphology, somatic doubling and secondary association in *Acer platanoides* L. — Hereditas XVIII, pp. 145—173.
108. MEURMAN, O. und RANCKEN, G. 1932. Untersuchungen über die Chromosomenverhältnisse bei kultivierten Kartoffelsorten (*Solanum tuberosum* L.). — Soc. Sci. Fenn., Comm. Biol. III, 20, pp. 1—28.
109. MOFFETT, A. A. 1931. The chromosome constitution of the *Pomoideæ*. — Proceed. Roy. Soc. 108, pp. 423—446.
110. MORINAGA, T. 1934. Cyto-genetical studies on *Oryza sativa* L. I. — MORINAGA, T. and FUKUSHIMA, E.: Studies on the haploid plant of *Oryza sativa* L. — Japan. Journ. of Bot. 7, pp. 73—106.
111. MÜNTZING, A. 1928. Pseudogamie in der Gattung *Potentilla*. — Hereditas XI, pp. 267—283.
112. — 1931. Note on the cytology of some apomictic *Potentilla*-species. — Hereditas XV, pp. 166—178.
113. — 1933 a. Apomictic and sexual seed formation in *Poa*. — Hereditas XVII, pp. 131—154.

114. MÜNTZING, A. 1933 b. Studies on meiosis in diploid and triploid *Solanum tuberosum* L. — Hereditas XVII, pp. 223—245.
115. — 1933 c. Quadrivalent formation and aneuploidy in *Dactylis glomerata*. — Bot. Notiser 1933, pp. 198—205.
116. — 1935 a. Cyto-genetic studies on hybrids between two *Phleum* species. — Hereditas XX, pp. 103—136.
117. — 1935 b. Berättelse över verksamheten vid Sveriges Utsädesförenings kromosomavdelning under tiden 1 oktober 1931—30 september 1935. — Sveriges Utsädesförenings Tidskr. 1935, pp. 305—320.
118. — 1936. The evolutionary significance of autopolyploidy. — Hereditas XXI, pp. 263—376.
119. — 1937. The effects of chromosomal variation in *Dactylis*. — Hereditas XXIII, pp. 113—235.
120. NAKAJIMA, G. 1930. On the chromosome number in some agricultural plants. — Japan. Journ. of Genetics 5, pp. 172—176.
121. — 1931. The chromosome number in cultivated and wild Angiosperms. — Bot. Magazine, Tokyo, 45, pp. 7—11.
122. — 1933. Chromosome number in some Angiosperms. — Japan. Journ. of Bot. 9, pp. 1—5.
123. NAKATOMI, S. 1923. Difference of chromosomes in various races and mutants of rice. — Japan. Journ. of Genetics 2, pp. 107—115.
124. NANDI, H. K. 1936. The chromosome morphology, secondary association and origin of cultivated rice. — Journ. of Genetics 33, pp. 315—336.
125. NATIVIDADE, J. V. 1937. Recherches cytologiques sur quelques espèces et hybrides du genre *Quercus*. — Boletim da Sociedade Broteriana, Ser. II, 12, pp. 21—92.
126. NAVASHIN, M. 1925. Morphologische Kernstudien der *Crepis*-Arten in bezug auf die Artbildung. — Zeitschr. f. Zellforsch. und mikr. Anat. 2, pp. 98—111.
127. — 1928. »Amphiplastie», eine neue karyologische Erscheinung. — Verh. der V. intern. Kongr. f. Vererb.-Wissensch. Zeitschr. f. indukt. Abstamm.- und Vererb.-Lehre, Suppl.-Band 2, pp. 1148—1152.
128. — 1934. Chromosome alterations caused by hybridization and their bearing upon certain general genetic problems. — Cytologia 5, pp. 169—203.
129. NEBEL, B. R. 1931. Recent findings in cytology of fruits. (Cytology of *Pyrus*). — Proceed. Amer. Soc. Hort. Sci. 27, pp. 406—410.
130. — 1933. Chromosome numbers in aneuploid apple seedlings. — New York State Agri. Exp. Stat., Techn. Bull. 209, pp. 1—12.
131. NEWTON, W. C. F. and DARLINGTON, C. D. 1929. Meiosis in polyploids. — Journ. of Genetics 21, pp. 1—56.
132. NILSSON, FR. 1933. Ein spontaner Bastard zwischen *Festuca rubra* und *Lolium perenne*. — Hereditas XVIII, pp. 1—15.
133. — 1935. Amphipolyploidy in the hybrid *Festuca arundinacea* × *gigantea*. — Hereditas XX, pp. 181—198.
134. NISHIYAMA, I. 1934. The genetics and cytology of certain cereals. VI. Chromosome behaviour and its bearing on inheritance in triploid *Avena* hybrids. — Mem. of the Coll. of Agri., Kyoto Imp. Univ., Genet. Ser. III, 32, pp. 1—157.

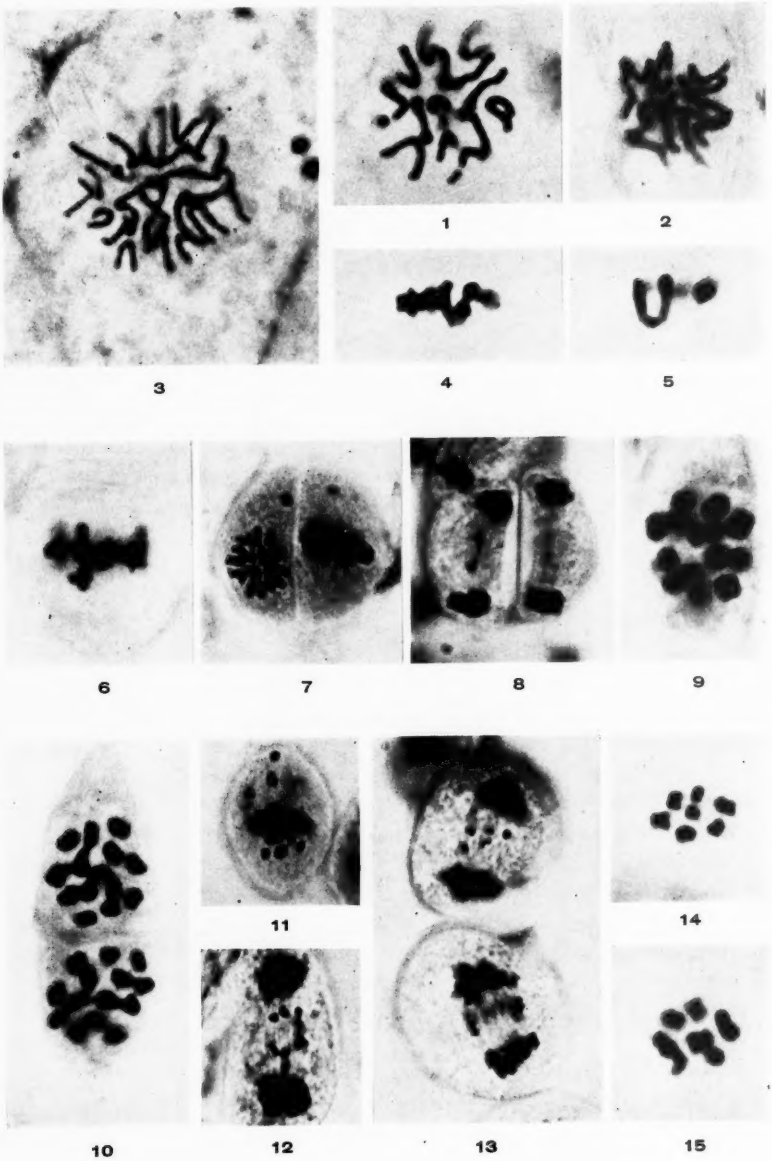
135. RANCKEN, G. 1934. Zytologische Untersuchungen an einigen wirtschaftlich wertvollen Wiesengräsern. — Acta Agralia Fennica 29, pp. 1—92.
136. RANDOLPH, L. F. 1928. Chromosome numbers in *Zea mays* L. — Cornell Univ. Exp. Stat., Mem. 117, pp. 1—44.
137. REUTER, E. 1930. Beiträge zu einer einheitlichen Auffassung gewisser Chromosomenfragen. — Acta Zoologica Fennica 9, pp. 1—487.
138. ROHWEDER, H. 1934. Beiträge zur Systematik und Phylogenie des Genus *Dianthus* unter Berücksichtigung der karyologischen Verhältnisse. — Bot. Jahrbücher 66, pp. 249—369.
139. ROSENBERG, O. 1926 a. Zum Mechanismus der diploiden Kernteilung in Pollenmutterzellen. — Arkiv för Botanik 20 B, No. 3, pp. 1—5.
140. — 1926 b. Über die Verdoppelung der Chromosomenzahl nach Bastardierung. — Ber. der deutschen bot. Gesellsch. 44, pp. 455—460.
141. — 1927. Die semiheterotypische Teilung und ihre Bedeutung für die Entstehung verdoppelter Chromosomenzahlen. — Hereditas VIII, pp. 305—338.
142. SAKAI, K. 1935. Chromosome studies in *Oryza sativa* L. I. The secondary association of the meiotic chromosomes. — Japan. Journ. of Genetics 11, pp. 145—156.
143. SANSOME, F. W. and PHILP, J. 1932. Recent advances in plant genetics. — London.
144. SAX, K. 1931. The origin and relationship of the *Pomoideæ*. — Journ. of the Arnold Arboretum 12, pp. 1—22.
145. SCHNARF, K. 1929. Embryologie der Angiospermen. — Handb. d. Pflanzenanat., Berlin.
146. SCHOLANDER, P. F. 1934. Vascular plants from northern Svalbard with remarks on the vegetation in North-East Land. — Skrifter om Svalbard og Ishavet 62, pp. 1—153. Oslo.
147. SENJANINOVA-KORCZAGINA, M. V. 1930. Karyo-systematical investigation of the genus *Ægilops*. — Proceed. U.S.S.R. Congr. of Genet., Plant- and Animal-Breeding, Leningrad, 2, pp. 453—466.
148. SHIMOTOMAI, N. 1931. Über die abnorme Reduktionsteilung in P.M.Z., die einen riesigen Kern oder überzählige Zwergkerne enthalten. — Bot. Magazine, Tokyo, 45, pp. 356—363.
149. — 1933. Zur Karyogenetik der Gattung *Chrysanthemum*. — Journ. of Sci. of the Hiroshima Univ., Ser. B, Div. 2, Vol. 2, pp. 1—100.
150. SIMONET, M. 1935. Conjugaison autosyndétique des chromosomes à la méiose de quelques hybrides interspécifiques d'*Iris*. — Bull. Biol. de la France et de la Belgique 69, pp. 178—212.
151. SMITH, H. 1914. *Catabrosa concinna* TH. FR. **algidiformis* nov. subsp. und ihre Nächstverwandten. — Svensk Bot. Tidskr. 8, pp. 245—252.
152. SMITH, L. 1936. Cytogenetic studies of *Triticum monococcum* and *T. ægilopoides*. (Abstract.) — Amer. Nat. 70, p. 66.
153. STENAR, H. 1932. Parthenogenesis in der Gattung *Calamagrostis*. — Arkiv för Botanik 25 A, No. 6, pp. 1—8.
154. STOLZE, K. V. 1925. Die Chromosomenzahlen der hauptsächlichsten Getreidearten. — Bibliotheca Genetica 8, pp. 1—71.
155. STÄHLIN, A. 1929. Morphologische und zytologische Untersuchungen an Gramineen. — Wiss. Archiv f. Landw., A. Pflanzenbau 1, pp. 330—398.

156. SWESCHNIKOWA, I. 1929 a. *Vicia sativa* L. and *Vicia cracca* L. — Ann. Timir. Ag. Acad. (Moscow) 4, pp. 1—22.
157. — 1929 b. Reduction division in the hybrids of *Vicia*. — Proceed. U.S.S.R. Congr. of Genet., Plant- and Animal-Breeding, Leningrad, 2, pp. 447—452.
158. TAYLOR, W. R. 1924. The smear method for plant cytology. — Bot. Gazette 78, pp. 236—238.
159. — 1925. Chromosome constrictions as distinguishing characteristics in plants. — Amer. Journ. of Bot. 12, pp. 238—244.
160. — 1926. Chromosome morphology in *Fritillaria, Alstroemeria, Silphium,* and other genera. — Amer. Journ. of Bot. 13, pp. 179—193.
161. THOENES, H. 1929. Morphologie und Anatomie von *Cynosurus cristatus* und die Erscheinung der Viviparie bei ihm. — Bot. Archiv 25, pp. 284—346.
162. TINCKER, M. A. H. 1925. The effect of length of day upon the growth and reproduction of some economic plants. — Ann. of Bot. 39.
163. TISCHLER, G. 1918. Untersuchungen über den Riesenwuchs von *Phragmites communis* var. *Pseudonax*. — Ber. der deutsch. bot. Ges. 36, pp. 549—558.
164. — 1927. Pflanzliche Chromosomen-Zahlen. — Tab. Biol. Period. 4, pp. 1—83.
165. — 1929. Revisionen früherer Chromosomenzählungen und anschliessende Untersuchungen. — Planta 8, pp. 685—697.
166. — 1931. Pflanzliche Chromosomen-Zahlen. — Tab. Biol. Period. 7, pp. 109—126.
167. — 1934. Die Bedeutung der Polyploidie für die Verbreitung der Angiospermen. Bot. Jahrb. 67, pp. 1—36.
168. — 1936. Pflanzliche Chromosomen-Zahlen. — Tab. Biol. Period. 12, pp. 57—115.
169. TJEBBES, K. 1931. Polymerism. — Bibliogr. Genetica 8, pp. 227—268.
170. TURESSON, G. 1926. Studien über *Festuca ovina* L. I. Normalgeschlechtliche, halb- und ganzvivipare Typen nordischer Herkunft. — Hereditas VIII, pp. 161—206.
171. — 1927. Contributions to the genecology of glacial relics. — Hereditas IX, pp. 81—101.
172. — 1930. Studien über *Festuca ovina* L. II. Chromosomenzahl und Viviparie. — Hereditas XIII, pp. 177—184.
173. — 1931. Studien über *Festuca ovina* L. III. Weitere Beiträge zur Kenntnis der Chromosomenzahlen viviparer Formen. — Hereditas XV, pp. 13—16.
174. WANSCHER, J. H. 1934. The basic chromosome number of the higher plants. — The New Phytologist 33, pp. 101—126.
175. WEXELSEN, H. 1934. Quantitative inheritance and linkage in barley. — Hereditas XVIII, pp. 307—348.
176. WINKLER, H. 1920. Verbreitung und Ursache der Parthenogenesis im Pflanzen- und Tierreiche. — Jena.
177. ZOLLIKOFER, C. 1930. Zur Fortpflanzung von *Poa alpina* L. — Jahrb. der St. Gallischen Gesellsch. 65, pp. 99—117.
178. ÅKERBERG, E. 1936 a. Studien über die Samenbildung bei *Poa pratensis* L. — Bot. Notiser 1936, pp. 213—280.
179. — 1936 b. Bastard mellan *Poa pratensis* L. × *Poa alpina* L., artificiellt framställd. — Bot. Notiser 1936, pp. 563—566.

CONTENTS.

I. Introduction 265
II. Material and methods 269
III. Description 274
1. *Alopecurus alpinus* SM. 274
2. *Arctagrostis latifolia* (R. BR.) GRISEB. 278
3. *Arctophila fulva* (TRIN.) RUPR. 279
4. *Calamagrostis neglecta* (EHRH.) P. B. 279
5. *Deschampsia alpina* ROEM. et SCHULT. 284
6. *Dupontia Fisheri* R. BR. 288
7. *Dupontia Fisheri* R. BR. var. *psilosantha* (RUPR.) SCHOL. 290
8. *Festuca rubra* L. var. *arenaria* (OSB.) E. FRIES 291
9. *Festuca ovina* L. var. *brevifolia* (R. BR.) HART. 293
10. *Festuca ovina* L. var. *vivipara* L. 296
11. *Hierochloe alpina* (LILJEBL.) ROEM. et SCHULT. 301
12. *Phippsia algida* (SOLAND.) R. BR. 301
13. *Phippsia concinna* (TH. FR.) LINDEB. 302
14. *Phippsia concinna* (TH. FR.) LINDEB. var. *algidiformis* (SMITH) HOLMB. 303
15. *Poa abbreviata* R. BR. 307
16. *Poa alpigena* (E. FRIES) LINDM. 308
17. *Poa alpigena* (E. FRIES) LINDM. var. *colpodea* (TH. FRIES) SCHOLANDER 311
18. *Poa alpigena* (E. FRIES) LINDM. var. *vivipara* (MALMGR.) SCHOLANDER 311
19. *Poa glauca* VAHL 314
20. *Poa alpina* L. var. *vivipara* L. 315
21. *Poa arctica* R. BR. 316
22. *Poa arctica* R. RR. var. *vivipara* (MALMGR.) SCHOLANDER 316
23. *Puccinellia angustata* (R. BR.) RAND. et REDF. 318
24. *Puccinellia phryganodes* (TRIN.) SCRIBN. et MERR. 320
25. *Puccinellia Vahliana* (LIEBM.) SCRIBN. et MERR. 321
26. *Trisetum spicatum* (L.) RICHT. 326

IV. Discussion 329
1. Chromosome morphology 329
2. The original basic chromosome number in grasses 332
A. Evidence from secondary association of the chromosomes at meiosis 332
B. Evidence from the formation of quadrivalents in diploids and bivalents in mono-haploids, and the unexpected conjugation in hybrids 337
C. Evidence from chromosome morphology 339
D. Evidence from genetic observations 341
E. Evidence from the now existing basic numbers and their multiples 342
F. The hypothesis of AVDULOV 343
G. Summarizing remarks 345
3. The occurrence of polyploidy in the arctic grasses 346
4. The occurrence of vivipary in the arctic grasses 349
Summary 364
Explanation of Plate I 367
Literature cited 367


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

DER EVOLUTIONSGEDANKE UND DIE VERGANGENE PFLANZENWELT

VON *HERIBERT NILSSON*

BOTANISCHES INSTITUT, LUND

(Vortrag, vom Verfasser als Vorsitzenden der »Kungl. Fysiografiska Sällskapet» in Lund bei ihrer Jahresfeier am 2. Dezember 1937 gehalten)

WENN ein neuer, grosser Gedanke aufgeworfen wird, verursacht er anfangs einen Gedankenstrom, der alles umwirbelt. Ganz natürlich ruft er deshalb auch einen Widerstand hervor. Bald aber merkt man, dass er neue Gesichtspunkte darbietet, neue Forschungswege öffnet. Und so wird nach einiger Zeit die ganze Forschung der betreffenden Disziplin auf ein einziges Ziel gerichtet, nämlich den Ausbau und die Vervollkommnung des neuen Gedankengebäudes, das bald wie eine stolze Burg mitten in einem alten Anbau hervortritt.

So ist auch der Evolutionsgedanke, seitdem er durch DARWIN lebendig gemacht wurde, zu einer Gedankenschaffung von riesigen Proportionen herangewachsen. Er beherrscht nicht nur alle Disziplinen der Biologie, sondern er ist auch auf die exakten Naturwissenschaften angewendet worden. Vor allem hat er indessen soziale Beziehungen gefunden. Mit der Theorie der Evolution brach eine neue Zeit, die der Gedankenfreiheit, an. Von ihrer Burg wurden die Waffen im Kampfe der sozialen Evolution geholt. Die Theorie brauchte allmählich keine wissenschaftlichen Beweise mehr, sie trug sich selbst durch ihre Gedankenmacht und ihre praktischen Konsequenzen. Sie wurde als etwas selbstverständliches betrachtet. Sie wurde zu einem Axiom erhoben.

Sagt man deshalb nun: »Es scheint mir, als ob die Burg sich zu setzen angefangen hätte», so wird geantwortet: »Ja, aber weisst du denn nicht, welche Rolle dieses Gebäude gespielt hat und noch spielt!»

Sagt man weiter: »Ich sehe gefährliche Risse in den Grundmauern», so antwortet man: »Ja, aber hast du denn niemals gesehen, welch ein schönes Gebäude es ist!»

Während den letzten drei Dezennien hat die Genetik der Artbildungsforschung ein neues und überaus reiches Material zugeführt. Aus diesem geht hervor, dass die Organismen aus konstanten Grundelementen aufgebaut sind. Diese Entdeckung stürzt die frühere Auffassung

der gleitenden Entwicklung ganz um. Denn äussere Faktoren können dann nicht, wie man meinte, den Organismus dauernd verändern, erworbene Eigenschaften können nicht erblich sein. Falls eine Variabilität eintreten soll, so muss ein Grundelement, ein Gen, ein biologisches Atom, wie man nun diese konstante Einheit nennen will, verändert werden.

Kennt die exakte Vererbungsforschung nun keine solchen Variationen? Gewiss, schon fast unzählige. Aber sie haben alle das gemeinsam, dass sie wahrscheinlich nicht neu sind. Einige sind Segreganten komplizierter Spaltungen (fester Koppelungen), andere Chimärenderivanten. Wieder andere sind Chromosomenaberranten oder Genmutanten. Sie können experimentell hervorgebracht werden, treten aber auch spontan in der Natur auf. Da man für die letzteren keine Induktionsquelle hat finden können, da sie aber *stetig* in einem gewissen Prozentsatz aus der Art derivieren, hat man sie, wie DE VRIES, aus labilen Genen abgeleitet oder, wie z. B. TIMOFÉEFF-RESSOVSKY ganz neulich in einem Vortrag hier in Lund sehr klar und exakt diese Meinung formulierte, man hat die Ursache ihres Auftretens »einer statistischen Instabilität des Gens» zugeschrieben. Hieraus folgt aber, dass sie dann auch so alt wie die Art sein müssen. Sie sind also *nicht neu.*

Da nun diese Mutanten alte Varianten sind, weshalb haben sie sich nicht durchgesetzt? Hat man mit ihnen gearbeitet, so befindet man sich hinsichtlich der Antwort nicht in Verlegenheit. Sie haben eine *geringere Vitalität* als die Mutterart. Sie haben deshalb keinen Selektionswert. Sie kommen und verschwinden, werden in einem Naturbestand ausgemerzt, werden erst unter Kulturverhältnissen beobachtet und wirken hier scheinbar neu. Auf sie eine Evolution aufzubauen ist deshalb mehr als gewagt. Die experimentellen Resultate der Artbildung geben deshalb für eine *fortgesetzte* Evolution keine Anhaltspunkte.

Aber eine Evolution muss wohl jedenfalls früher stattgefunden haben? Ja, eine solche in unsrem Gehirn spekulativ zu ordnen ist sehr leicht, ebenso leicht wie es früher war eine fortgesetzte Evolution anzunehmen, solange der keine Experimentalforschung im Wege stand. Eine Entwicklung von der Amöbe zum Menschen ist ja ganz natürlich, denn auch der Mensch fängt als eine einzige Zelle an, sagt man. Hier liegt keine Schwierigkeit für den Gedanken in bezug auf Anfang und Ende der Entwicklung. Schwieriger ist es aber, die Entwicklung von *Taraxacum* zu *Sonchus* oder umgekehrt sich vorzustellen, denn man findet bei dieser und ähnlichen Überlegungen, dass primitive und entwickelte Eigenschaften so vermengt sind, dass man die Frage nicht

entscheiden kann. Die Schlussfolgerung ist immer, dass die beiden Genera aus einer gemeinsamen Stammform sich entwickelt haben. Von dieser Art, Evolutionsfragen zu lösen, betragen die Ausnahmen nicht eine Promille. Unsre heimischen Gattungen der Familie *Compositæ* sind 56. Für alle dürften wir bei einer evolutionären Überlegung nur zu dem Resultat kommen, dass sie von einer gemeinsamen Elternform abstammen. Hier versagt unsre Sicherheit ganz.

Das Beweismaterial für die Evolutionstheorie ist ja zum grössten Teil auf einer Ähnlichkeit zwischen kürzeren oder längeren Serien in bezug auf äussere oder innere Struktur aufgebaut. Aus Ähnlichkeit schliesst man also auf gemeinsame Abstammung. Ähnlichkeit braucht aber nicht mehr als ähnliche Konstitution zu bedeuten. Das ist in den exakten Naturwissenschaften selbstverständlich.

Beleuchtend für diese Frage ist die hervorragende Entdeckung von HOFMEISTER in der Mitte des vorigen Jahrhunderts über die Homologien der Phanerogamen und Kryptogamen. LINNÉ und spätere Forscher hatten eine grosse Kluft zwischen diesen beiden Gruppen des Pflanzenreiches gesehen. HOFMEISTER wies aber in genialer Weise nach, dass man in embryologischer und befruchtungsmechanischer Hinsicht eine ganz ausserordentlich schöne und kontinuierliche Übergangsserie zwischen alle kormophyten Pflanzen hat. Die Serie Moose—Farne—Wasserfarne—Cycadeen—Koniferen—Angiospermen zeigte in bezug auf den Generationswechsel und die sukzessive Reduktion des Prothalliums sowie die Ausbildung der Archegonien so ausgeprägte Übereinstimmungen, dass man ihre intime Zusammengehörigkeit nicht in Zweifel ziehen konnte. Eine konstitutionelle Verwandtschaft liegt hier ganz offenbar vor.

HOFMEISTERS Untersuchungen sind prädarwinistisch. Als nun aber ein Paar Jahrzehnte später evolutionäre Gedankengänge stabilisiert wurden, führte man die konstatierten Konstitutionsserien in evolutionäre Abstammungsserien über. Eine Entwicklung Moose—Angiospermen mit den genannten Zwischenstufen wurde behauptet. Mit der Reduktion der Anzahl Sporangien und dem festen Anschliessen des Indusiums an das zuletzt allein übriggebliebene wurde der Sorus in eine Samenanlage umgewandelt. Ganz sukzessiv entstand, als die Krone der Entwicklung, die Samenanlage. Aus Sporenpflanzen entwickelten sich Samenpflanzen. Und in keiner anderen Abteilung des Pflanzenreiches fand man einen so überzeugenden Beweis einer sukzessiven Evolution als in HOFMEISTERS Serie der Entwicklung der Kormophyten. Die Ursache der Veränderung, den treibenden Faktor der Um-

wandlung, fand man auch ganz klar. Dieser bestand in einer Reduktion des Prothalliums, die durch ein Herabsetzen der induzierenden Feuchtigkeit während der fortschreitenden Erdperioden erklärt wurde.

So baut man also einen Stammbaum auf. Ist er wahrscheinlich? Jawohl, als Konstruktion ist er sehr wahrscheinlich. Ist er richtig? Das wissen wir nicht. Um dies zu entscheiden, müssen wir in den Dokumenten nachforschen, wo diese Evolution niedergeschrieben sein *muss*, nämlich in der geologischen Geschichte der Erde. Die Fossilien müssen die Hauptzüge dieser Entwicklung aufweisen. Wir können also die Frage ganz empirisch entscheiden.

Die niedrigste Stufe der kormophyten oder archegoniaten Pflanzen, die Moose, mussten wir zuerst erwarten. Da Farne schon in der Steinkohlenformation auftreten, sind die Moose noch früher zu erwarten. Man findet sie aber weder im Karbon noch früher. Im ganzen Paläozoikum sind sie nicht zu finden, auch nicht im älteren Mesozoikum. Erst in der Kreide sind sie sicher konstatiert worden. Vorfahren der Moose kennt man nicht.

Aber, sagt man, die Moose sind ganz zarte Gebilde, deren Erhaltung als Fossilien man kaum voraussetzen kann. Dies ist vielleicht richtig, insofern man mit Abdrucken rechnet. Wir haben aber vom Karbon zahlreiche Fossilien in den knollenförmigen Dolomiten (»coal balls») der produktiven Kohlenschicht, in denen auch sehr winzige Pflanzenreste ganz gut erhalten sind. Die Möglichkeit für ein Konservieren von Moosteilen ist hier ebensogross wie im Bernstein des älteren Tertiärs, wo Moose häufig sind. Da die Moose in den Wäldern ganze Bodendecken bilden und auch epiphytisch leben, ist es kaum möglich, dass sie, falls sie wirklich in den Steinkohlenwäldern existierten, einer fossilen Erhaltung entgehen konnten. Die als sehr alt aufgefassten Moose treten also erst sehr spät auf.

Älter sind gewiss die Farne. Man hat ja die Karbonzeit die Zeit der Farne genannt. Sie scheinen also sehr alt zu sein.

Das Studium der Karbonpflanzen während dieses Jahrhunderts hat indessen unser früher angenommenes Bild dieser Vegetation ganz verändert. Es hat sich nämlich gezeigt, dass die Bäume, die man für baumartige Farne hielt, gar nicht wie unsre rezenten Farne Sporenpflanzen sind. Sie sind etwas ganz anderes und ganz überraschendes — sie sind Samenpflanzen. Samenpflanzen mit Farnblättern, Pteridospermen. Der Samen ist vollkommen entwickelt, bezeichnet keine Zwischenstufe. Sie sind ebenso gute Samenpflanzen wie gewisse unsrer Gymnospermen.

Was bedeutet dann das Konstatieren dieser merkwürdigen Gruppe? Es bedeutet, dass schon im alten Paläozoikum Samenpflanzen auftraten. Aber sie sollten ja das Endglied der Entwicklung bezeichnen! Ja, unsrer Spekulation nach. Sie treten aber *unwiderlegbar* im Karbon auf, ja, noch früher scheint es, denn schon im Devon hat man sie konstatiert. Sie sind keine Seltenheiten. Sie treten nämlich in grossen Wäldern auf der ganzen nördlichen Halbkugel auf, und sie bilden eine bedeutende Komponente der Kohlenablagerungen.

Samenpflanzen, die höchste Entwicklungsform der Kormophyten, die wir erst in den letzten Perioden der Erde zu erwarten hätten, sind also schon im Karbon überaus reich vertreten. Das, wozu sich eine niedrigere Vegetation durch Millionen und wieder Millionen Jahre, ja Hunderte von Millionen Jahre, entwickeln sollte, nämlich Samenpflanzen, das ist schon im Devon fix und fertig.

Vielleicht wendet man ein, dass die vordevonischen Zeiträume der Erde ausserordentlich lang sind, so dass man doch eine langdauernde Entwicklung der Pteridospermen voraussetzen könnte. Nein, das ist nicht möglich. Denn während der vorhergehenden Silurperiode hatten wir keine Landpflanzen, auch keine Kormophyten. Schon an der Grenze einer Landvegetation gibt es Pflanzen mit wohlausgebildeten Samen, wie wir sie bei jetzt lebenden Formen sehen. Die Vegetation dieser frühesten Epochen enthielt also *auch* Samenpflanzen.

Unsre *rezenten* Farne passen sehr gut als Stammformen für Samenpflanzen. Aber diese treten schon gleichzeitig mit den Farnen im Paläozoikum auf. Ja, es fragt sich, ob wir im Devon schon echte Farne haben, während das Auftreten von Pteridospermen nicht bezweifelt werden kann.

Sich ein evolutionäres Bild aus den angeführten Tatsachen zu konstruieren geht überhaupt nicht. Denn für das, was gleichzeitig auftritt, ist es sinnlos, von einer Evolution zu reden. Und wenn ein als hochentwickelt angesehener Typus wie die Samenpflanze schon am Morgen der Entstehung einer Landvegetation da ist, so braucht man keine Evolution über hunderte Millionen von Jahren um zu ihm in der rezenten Vegetation zu kommen. Das ist ja selbstverständlich.

Die erwähnte eigentümliche Vegetation der Pteridospermen verschwand nebst einer unzähligen Menge anderer eigentümlichen Typen, die natürlich ganz wie die rezente Vegetation in »höhere» und »niedrigere» sortiert werden können, mit dem Paläozoikum oder jedenfalls Anfang des Mesozoikums. Es entsteht eine ganz neue Erdflora. Auch diese enthält Samenpflanzen. Diese sind sogar gleichzeitig Blüten-

pflanzen. Von unsren Blütenpflanzen sind sie aber so verschieden wie eine gedachte Vegetation am Mond. Man hat oft versucht, die hypothetische Blüte der Vorfahren unsrer angiospermen Blütenpflanzen zu konstruieren, aber niemand ist auf einen so phantastischen Gedanken gekommen, dass er die Blüte der mesozoischen *Bennettitales* sich annähernd vorgestellt hätte. Staubblätter, die Miniaturblättern von Farnen ähneln, kombiniert mit Fruchtblättern, die auf nur einen Stiel mit einer Samenanlage reduziert sind und so eine Art Sammelfrucht aus speziellen sterilen Fruchtblättern — das liegt alles ganz ausserhalb des Bauplanes jeder jetztzeitigen Blütenpflanze. Und ebenso stark weichen sie von den paläozoischen Samenpflanzen ab, bei denen die Samen gewöhnlich noch nicht an blütenartig zusammengedrängten Sporophyllen sassen, sondern am Rand grosser Blätter, die den vegetativen Blättern mehr oder minder ähnelten.

Wir haben in den Bennettiten einen ganz neuen Typus von Samenpflanzen, der weder selbst eine Übergangsform zwischen den paläozoischen und den rezenten Spermatozyten darstellt noch paläontologisch mit diesen durch Serien von Zwischenformen verbunden ist. Die drei Gruppen bezeichnen drei ganz freistehende Konstitutionstypen, Baupläne, Reaktionskomplexe, wie man es nun ausdrücken will.

Die *Bennettitales* bildeten die weit vorherrschende Vegetation des ganzen Mesozoikums. Sie waren über die ganze Erde verbreitet. Eine neue Flora ist entstanden. Sie bildet aber keine Vorstufe zu unsrer heutigen dominierenden angiospermen Flora.

Wenn dem so ist, wann entstand dann unsre rezente Vegetation? Und welche sind die Stammeltern der Angiospermen?

Die erste Frage können wir nunmehr ganz befriedigend, fast exakt beantworten. Die Angiospermen entstanden in den oberen Schichten der unteren Kreide.

Auch die andere Frage können wir beantworten, obgleich niemand gern eine direkte und offene Antwort geben will. *Wir kennen keine Vorfahren der Angiospermen.*

In der älteren Kreide erfolgte eine erstaunliche Veränderung der ganzen Vegetation. Die oben erwähnte mesozoische Flora findet man noch in den untersten Schichten. In den obersten tritt eine ganz andere, ausserordentlich abweichende Pflanzenwelt auf, eine vorherrschend angiosperme. Unsre Gattungen wie *Quercus*, *Platanus*, *Artocarpus* und *Cinnamomum* hat man hier identifiziert. In der mittleren und oberen Kreide, aus der mehr und reichere Funde vorliegen, kommen Gattungen aus fast dem ganzen heutigen System zum Vorschein, Dikotylen und

Monokotylen, Choripetalen und Sympetalen. Wir finden Repräsentanten unsrer Familien und Gattungen, in gewissen Fällen offenbar auch unsre Arten, obgleich für die letzteren eine Identifizierung natürlich schwieriger ist.

Diese Flora steht im intimsten Zusammenhang mit der heute lebenden. Eigentümlich ist auch, dass sie keine primitiven Vorläufer unsrer Angiospermen repräsentiert. Man findet sowohl andere Arten und auch Gattungen als die rezenten, aber kaum andere Familien. Die Kreideflora ist *reicher*, aber *nicht primitiver* als die nun lebende. Die Angiospermen bilden die dominierende Komponente der Vegetation, also ganz wie heute. In gewissen Fundstätten der jüngeren Kreide sind sie in einem Prozentsatz von 70—90 % festgestellt worden. Sie sind auch über die ganze Welt verbreitet. Man kennt Funde aus z. B. Nordamerika, Grönland, Sibirien, Sachalin, Böhmen, Portugal, Madagaskar, Patagonien.

In der Kreideperiode quellen die Angiospermen förmlich hervor. Die früher dominierenden Bennettiten sind verschwunden. Eine ganz neue Vegetation steht da, schon ganz fertig, schon überreich.

Diese Flora lebt noch. Während des ganzen Känozoikums hat sie fortbestanden, einen Zeitraum, den man auf 50 Jahrmillionen schätzt. In diesem Fall ist es nicht schwer, die Kontinuität zu konstatieren. Diese ist ebenso ungebrochen wie das Aufhören jedes Anschlusses in der unteren Kreide vollkommen ist. Schon eine alttertiäre Flora von Wight besteht zu 89 Prozent aus jetzt lebenden Gattungen. Unsre Flora zeigt aber eine geringere Mannigfaltigkeit, eine geringere Variabilität als die alttertiäre. Weit davon, eine Weiterentwicklung dieser aufzuweisen, stellt sie eine Depauperierung, eine *selektive Reduktion* dieser dar.

Unser Versuch, eine der grössten und sichersten Evolutionsserien durch paläontologische Beweise zu verifizieren, hat ganz und gar versagt. Denn die Moose und die Angiospermen, die niedrigste und höchste Gruppe, erscheinen gleichzeitig, beide spät. Samenpflanzen, die das Endglied der Entwicklung bezeichnen sollten, sind schon in aller ältester Zeit zu finden, fast sobald überhaupt Landpflanzen auftreten. Unsre heutige angiosperme Flora trat ganz unvermittelt in der älteren Kreide auf, ohne Vorfahren, und in ähnlicher Weise isoliert, ohne Zwischenformen und ohne Vorfahren, stehen die früheren Erdfloren. Das alles macht ja die angenommene Evolution der Kormophyten ungereimt und führt auch ganz konsequent und unwiderstehlich dazu, eine Evolution überhaupt als unwahrscheinlich zu betrachten. Die grossen Erdfloren

scheinen als abgegrenzte Variationssphären aufzutreten. Sie zeigen nur Sukzession, keine Evolution.

Aber, wendet man ein, dieser Schluss ist vielleicht berechtigt auf Grund unsrer jetztigen Kenntnis der fossilen Pflanzenwelt. Diese ist aber allzu fragmentarisch, um für so weitgehende Schlussfolgerungen benutzt werden zu können.

Nein, wage ich zu sagen. Denn, wenn wir auch nur einen Bruchteil der vergangenen Vegetation kennen, so gibt uns dieser für jede Periode der Erde ein durchschnittliches Bild der *wahren* Flora, was erstens mehr bedeutet als alle spekulativen Stammbaumkonstruktionen von DARWIN bis jetzt, und weiter hat sich ja gezeigt, dass das Material ausreichend ist, um einen auffallenden Hiatus zwischen den Erdfloren zu demonstrieren und die grosse Mannigfaltigkeit dieser festzulegen. Findet man also im ganzen Mesozoikum vor der Kreide keine einzige sichere angiosperme Pflanze — und darin scheinen alle Phytopaläontologen einig sein, dass dieser Fund noch nicht gemacht worden ist — so wäre es ja ein Wunder aller Wunder, wenn *gerade Angiospermen* nicht gefunden werden konnten, da sie dann plötzlich massenhaft in der Kreide konstatiert werden können. Nur eine wahrscheinliche, ja vernünftige Deutung dieser Tatsache verbleibt: Wir haben keine Angiospermen vor der Kreide. *Deshalb* finden wir sie nicht. Die Angiospermen sind in dieser letzteren Zeitperiode entstanden.

Es ist ganz offenbar, dass die Forschungsresultate, die durch die Genetik und durch die Paläobotanik während dieses Jahrhunderts erhalten worden sind, nicht von der Evolutionstheorie als konstruktive Theorie umfasst werden können. Die heutigen Arten scheinen zwar variabler zu sein, als man früher glaubte, weil ihr rekombinatorischer Biotypeninhalt sehr gross ist, aber auch konstanter als sie auf Grund des evolutionären Gedankenganges erachtet wurden, weil sie weder von äusseren Faktoren noch von einer Mutabilität ohne Selektionswert verändert werden. Sie sind deshalb als Variationssphären konstant. Ganz dasselbe lehrt uns die Angiospermenflora. Familien und Gattungen sind bei dem ersten Konstatieren dieser Flora weder primitiv noch stark miteinander verflochten. Auch diese höheren systematischen Gruppen scheinen konstant umschriebene Variationssphären darzustellen. LINNÉs Auffassung von der Konstanz der Arten scheint kein Dogma, sondern eine Tatsache zu sein.

Unerklärlich sind auch vom Ausgangspunkt der Evolutionstheorie die durchaus ganz verschiedenen grossen Erdfloren während den differenten geologischen Epochen. Sie stehen ohne Zwischenglieder da, auf

einmal fertig und auf einmal in grösster Vielförmigkeit. Einmal um das andere tritt eine ganz neue Vegetation auf, ohne dass wir postulierte Vorfahren finden können. Diese Sukzession ohne Evolution mit Zwischenperioden von tabula rasa erinnert an die Auffassung des Entstehens der Organismenwelt von CUVIER.

Durch MENDEL haben wir eine ganz neue Auffassung von den Begriffen der Artbildung und der Variation erhalten. Sie sind als die Synthese und die Analyse biologischer Grundelemente zu betrachten, die ebenso konstant wie die Atome der Chemie sind. Mit diesen kann der Biologe ebenso sicher experimentieren wie der Chemiker oder Physiker mit Atomen und Quanten. Wir können in der Biologie nunmehr exakt vorgehen, wir brauchen deshalb nicht mehr weder teleologisch noch evolutionär zu denken.

Mit einem Festhalten an einer Theorie, die mit den Tatsachen des gewaltigen Forschungsmaterials dieses Jahrhunderts auf dem Gebiet der Artbildung nicht übereinstimmt, gewinnt man nichts. Mit LAMARCK, DARWIN und DE VRIES kommen wir nicht weiter. LINNÉ, CUVIER und MENDEL bezeichnen sicher den Gedankenweg, den wir einzuschlagen haben, um zu einer neuen Totalauffassung der Artbildung zu gelangen, wo wir nicht nur die Naturphilosophie sondern auch die evolutionäre Romantik fallen lassen müssen und nur auf den exakten Momenten der Biologie bauen dürfen. Das bedeutet, dass wir weder eine *creatio divina ex nihilo* akzeptieren, denn eine Synthese aus Nichts kennen wir nicht, noch eine *creatio darwiniana ex una cellula*, denn schon die ältesten biologischen Perioden enthalten Organismen von grösster und höchster Differenzierung.

In welcher gewaltsamen Synthese die biologischen Grundelemente konstituiert wurden wissen wir nicht, dass aber in dieser die Flora eines grossen geologischen Abschnittes der Erde sozusagen mit einem Schlage fertiggebildet wurde, niedrige wie höhere Arten, dafür haben wir augenfällige Beweise. Dies stimmt ja auch mit den Erfahrungen der exakten Naturwissenschaften, dass, wenn nur die Reaktionskomponenten vorhanden sind, so werden die komplizierten Endprodukte ebenso leicht wie die einfachen gebildet. Die Zeit bedeutet hierbei nichts. Diese Auffassung stimmt auch mit dem überein, was wir als die Horizontlinie in der naturwissenschaftlichen Forschung fühlen, nämlich dass alles Geschehen, in der biologischen wie in der atomalen Welt, einem grossen Gesetz folgt, nämlich dem Gesetz der grossen Zahlen.

DIE ERBLICHKEITSVERHÄLTNISSE DES MÄNNLICHEN DIMORPHISMUS BEI PARASEMIA PLANTAGINIS

VON *ESKO SUOMALAINEN*
GENETISCHES INSTITUT DER UNIVERSITÄT HELSINKI, FINNLAND

(Vorläufige Mitteilung)

IN mehreren Gegenden ihres Verbreitungsgebietes tritt *Parasemia plantaginis* nebeneinander in zwei scharf getrennten Männchenformen auf. Bei der einen (f. *typica*) ist die Grundfarbe der Hinterflügel klar gelb, bei der anderen (ab. *hospita* SCHIFF.) dagegen rein weiss. Zwischenformen sind nicht angetroffen worden. Beim Weibchen wechselt die Grundfarbe der Hinterflügel von rot bis rotgelb mit zahlreichen Übergängen. Ein weiblicher Dimorphismus ist also bei der Art nicht vorhanden. Über die verschiedenen Färbenformen von *Parasemia plantaginis* vgl. z. B. DEMAISON (1917) und SCHAWERDA (1906).

Die ausgeführten Kreuzungsversuche. — Die in meinen Versuchen zur Verwendung gekommenen *Parasemia plantaginis*-Individuen stammten aus der Gegend von Porvoo in Südfinnland, wo sowohl die gelbe als die weisse Männchenform häufig vorkommt. Die Nachkommen zweier im Juni 1937 erbeuteten, befruchteten Weibchen — das Männchen ist in beiden Fällen unbekannt — entwickelten sich noch im August—September des gleichen Jahres zu Imagines.

Zucht 1. ♀ (× ♂ unbekannt)			*Zucht 2.* ♀ (× ♂ unbekannt)		
F_1:	weisse ♂♂	2	F_1:	weisse ♂♂	4
	gelbe ♂♂	3		gelbe ♂♂	—
	♀♀	5		♀♀	5

Die Nachkommen reziproker Kreuzungen dieser F_1-Individuen hatten bis zum November—Dezember ihre Entwicklung vollendet. Von sechs ausgeführten Kreuzungen ergaben nur zwei Falter:

Zucht 3. ♀ (F_1-Individuum, Zucht 2) × weisses ♂ (ebenso)

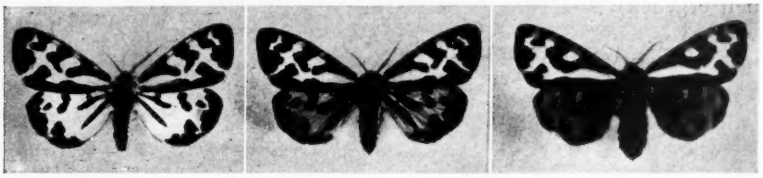
F_2:	weisse ♂♂	41
	gelbe ♂♂	10
	♀♀	24

Zucht 4. ♀ (F_1-Ind., Zucht 2) × gelbes ♂ (F_1-Ind., Zucht 1)

F_2:	weisse ♂♂	4
	gelbe ♂♂	6
	♀♀	4

Mit diesen F_2-Individuen wurden sieben Kreuzungen ausgeführt. Nur zwei ergaben Raupen, aber auch diese starben vermutlich zufolge Mangel an geeigneter Nahrung, die sich im Winter nicht beschaffen liess. Es ist daher die Fortsetzung der Kreuzungsversuche mit dem besprochenen Stamm nicht mehr möglich, doch hoffe ich Gelegenheit zu finden, die obigen Resultate in den nächsten Jahren mit Hilfe neuen Materials ergänzen zu können.

Besprechung der Versuchsergebnisse. — Die oben relatierten Versuche zeigen, dass die weisse Farbe der Hinterflügel beim Männchen



a *b* *c*

Fig. 1. *Parasemia plantaginis* L. *a*: Weisses Männchen. *b*: Gelbes Männchen. *c*: Weibchen. (Ung. nat. Gr.)

dominant, die gelbe dagegen rezessiv ist. Nehmen wir an, dass ein Genpaar die differenten Formen erzeugt, m. a. W. dass es sich hier um eine monohybride Mendelspaltung handelt, so sind die weissen Männchen entweder *AA* oder *Aa*, die gelben *aa*. Das Weibchen kann gleichfalls *AA*, *Aa* oder *aa* sein; hier sind jedoch alle drei Formen phänotypisch gleich. Die Ergebnisse obiger Kreuzungen können unter dieser Voraussetzung folgendermassen erklärt werden:

Zucht 1. Das eine der Elterntiere ist vermutlich *Aa* und das andere *aa*. In der F_1-Generation müssten ebenso viel weisse (*Aa*) wie gelbe (*aa*) ♂♂ entstehen. Das Ergebnis: Weisse ♂♂: 2. Gelbe ♂♂: 3.

Zucht 2. Das eine der Elterntiere ist vermutlich *AA* und das andere *aa*. In der F_1-Generation müssten sämtliche ♂♂ weiss (*Aa*) sein. Das Ergebnis: Weisse ♂♂: 4. Gelbe ♂♂: 0.

Zucht 3. ♀ (*Aa*) × weisses ♂ (*Aa*). Es müssten weisse (*AA* und *Aa*) und gelbe (*aa*) ♂♂ im Verhältnis 3 : 1 entstehen. Das Ergebnis: Weisse ♂♂: 41. Gelbe ♂♂: 10.

Zucht 4. ♀ (*Aa*) × gelbes ♂ (*aa*). Es müssten ebenso viel weisse (*Aa*) und gelbe (*aa*) ♂♂ entstehen. Das Ergebnis: Weisse ♂♂: 4. Gelbe ♂♂: 6.

Obige Resultate zeigen deutlich, dass sich die beiden Männchenformen von *Parasemia plantaginis* nur in bezug auf ein einziges Genpaar unterscheiden. Es handelt sich also um eine *monohybride geschlechtskontrollierte Vererbung*; die weisse Flügelfarbe ist dabei dominant und die gelbe rezessiv.

Mit dem oben Angeführten steht das Versuchsergebnis WALTHERS (1927, S. 48) in gutem Einklang. Im Anschluss an seine Untersuchungen über den Melanismus der Schmetterlinge führte er u. a. auch mit *Parasemia plantaginis* folgende Kreuzungen aus (die Anzahl der beiden Männchenformen hat sich durch Berechnung aus den von WALTHER in seinen Versuchsresultaten angegebenen Zahlen der verschiedenen Formen ergeben):

Elter: ♀ (× ♂ unbekannt)

F_1:	weisse ♂♂	14
	gelbe ♂♂	18
	♀♀	22

Bei fortgesetzter Kreuzung eines Weibchens mit einem gelben Männchen (beide F_1) erhielt WALTHER:

F_2:	weisse ♂♂	12
	gelbe ♂♂	8
	♀♀	18

Betrachten wir die vorstehenden Zahlen, so erscheint es offenbar, dass das eine der Elterntiere *Aa*, das andere *aa* war. In der F_1-Generation müssten also ebenso viel weisse (*Aa*) wie gelbe (*aa*) Männchen auftreten, was auch in der Tat der Fall war (14 und 18). Das zur Kreuzung verwendete F_1-Weibchen war wohl heterozygotisch (*Aa*), das Männchen gelb (*aa*). Wieder müssten beide Männchenformen in gleicher Zahl erscheinen, was auch zutraf (12 und 8). WALTHER selbst schenkt diesem männlichen Dimorphismus von *Parasemia plantaginis* keine Beachtung, FORD (1937, S. 492) aber stellt auf Grund WALTHERS Ergebnisse fest, dass »*Hospita* is clearly behaving as a dominant here».

Schwieriger lassen sich dagegen die von PICTET (1928, S. 479—482) mit *Parasemia plantaginis* erhaltenen Kreuzungsresultate erklären. Er hat drei in verschiedenen Höhenlagen der Alpen heimische Rassen (»races») der genannten Art untersucht. Rasse I bewohnt die niedrig-

sten Lagen bei etwa 1700 m. Bei ihr ist die schwarze Zeichnung der Flügel sehr stark entwickelt. Die Hinterflügelfarbe der Männchen ist gelb. Rasse II hat ihre Verbreitung in einer Höhenlage von etwa 2700 m. Sie ist klein und hell, die Farbe der Hinterflügel der Männchen ist weiss. Die bei etwa 2200 m lebende Rasse III schliesslich ist gross mit klaren Farben. Die Männchen haben gelbe Hinterflügel. Sämtliche drei Rassen sind vollkommen konstant. PICTET behauptet festgestellt zu haben, Rasse III repräsentiere eine heterozygotische Form der Rassen I und II. Diese letzteren unterschieden sich voneinander nur in bezug auf ein Genpaar; die Eigenschaften von Rasse I sind dominant, die von Rasse II dagegen rezessiv. PICTET stellte weiter fest, dass bei Kreuzung von Rasse I und II sämtliche F_1-Individuen den Typus von Rasse III zeigen. In der F_2-Generation entstanden »en captivité» Individuen der Rassen I, III und II annähernd im Verhältnis 1 : 2 : 1; primäre Zahlenwerte sind nicht angegeben. Den Umstand, dass Rasse III in der Natur konstant auftritt, führt PICTET darauf zurück, dass in der Höhenlage von 2200 m die beiden homozygotischen Rassen lebensunfähig sind. PICTET fand demnach die gelbe Flügelfarbe des Männchens dominant und die weisse rezessiv, was völlig im Gegensatz zu den Resultaten meiner Versuche steht. Ohne die Stichhaltigkeit der Versuchsresultate PICTETs direkt bezweifeln zu wollen, kann ich dennoch nicht unterlassen, die Aufmerksamkeit auf einige Eigentümlichkeiten derselben zu lenken. Es erscheint höchst sonderbar, dass der Unterschied in einem Genpaar so mannigfaltige Unterschiede zwischen der Rasse I und II hervorrufen soll, wie sie z. B. in der Körpergrösse, in der Ausbreitung der schwarzen Flügelzeichnung, in der Farbe der Hinterflügel, in der Höhenlage ihres Verbreitungsgebietes u. s. w. in den Abbildungen von PICTET zum Ausdruck kommen. Ebenso eigentümlich erscheint, dass Höhenunterschiede von nur 500 m schon tötend wirken sollen. Da die beiden homozygotischen Formen in einer Höhenlage von 2200 m regelmässig sterben sollen, handelt es sich hier also um eine Art balanzierter Letalfaktoren. Diese wie auch einige andere Umstände legen die Vermutung nahe, dass PICTET seine Versuchsergebnisse allzusehr schematisiert hat und dass letztere noch einer Nachprüfung bedürfen. Möglich ist natürlich auch, dass die weissflügeligen Männchen PICTETs mit den in meinen Versuchen verwendeten genotypisch nicht übereinstimmen.

Der männliche Dimorphismus von *Parasemia plantaginis* stellt meines Wissens vorläufig den einzigen genetisch genauer analysierten Fall von männlichem Polymorphismus bei Insekten dar. Entsprechende

Fälle bei Weibchen sind dagegen schon mehrere bekannt, und zwar stammen auch hier die bekanntesten aus dem Kreise der Schmetterlinge. Bei einigen *Colias*-Arten (GEROULD, 1911, 1923) sowie bei *Argynnis paphia* (GOLDSCHMIDT und FISCHER, 1922) sind sämtliche Männchen einander gleich, die Weibchen treten aber in zwei Typen auf. Bei den schon klassisch gewordenen Fällen der tropischen *Papilio memnon* (DE MEIJERE, 1910) und *P. polytes* (FRYER, 1913) gibt es gleichfalls nur einerlei Männchen, aber dreierlei Weibchen. Alle diese Fälle entsprechen einander völlig, nur ist bei den *Colias*-Arten und *Argynnis paphia* bloss ein geschlechtskontrolliertes Genpaar vorhanden, bei den *Papilio*s gibt es aber ihrer zwei. Der von mir beschriebene Dimorphismus bei *Parasemia plantaginis* unterscheidet sich von den obigen darin, dass er durch ein Genpaar bedingt wird, das *nur beim Männchen* phänotypisch zum Ausdruck kommt.

ZITIERTE LITERATUR.

1. DEMAISON, L. 1917. Observations sur diverses variétés de *Parasemia plantaginis* L. — Bull. Soc. entom. France 1917, p. 255—258.
2. FORD, E. B. 1937. Problems of heredity in the Lepidoptera. — Biol. Rev. 12, p. 461—503.
3. FRYER, J. C. F. 1913. An investigation by pedigree breeding into the polymorphism of *Papilio polytes*, LINN. — Phil. Trans. Roy. Soc. London, B 204, p. 227—254.
4. GEROULD, J. H. 1911. The inheritance of polymorphism and sex in *Colias philodice*. — Amer. Nat. 45, p. 257—283.
5. — 1923. Inheritance of white wing color, a sex-limited (sex-controlled) variation in yellow Pierid butterflies. — Genetics 8, p. 495—551.
6. GOLDSCHMIDT, R. und FISCHER, E. 1922. *Argynnis paphia — valesina*, ein Fall geschlechtskontrollierter Vererbung bei Schmetterlingen. — Genetica 4, p. 247—278.
7. DE MEIJERE, J. C. H. 1910. Über JACOBSONS Züchtungsversuche bezüglich des Polymorphismus von *Papilio memnon* L. ♀ und über die Vererbung sekundärer Geschlechtsmerkmale. — Ztschr. f. ind. Abst.- u. Vererb.-lehre 3, p. 161—181.
8. PICTET, A. 1928. Les conditions du déterminisme des proportions numériques entre les composants d'une population polymorphe de Lépidoptères. — Rev. Suisse de Zool. 35, p. 473—505.
9. SCHAWERDA, K. 1906. [Formen von *Parasemia plantaginis* L.] — Verhandl. zool.-bot. Ges. Wien 56, p. 238—241.
10. WALTHER, H. 1927. Ueber Melanismus. — Iris 41, p. 32—49.

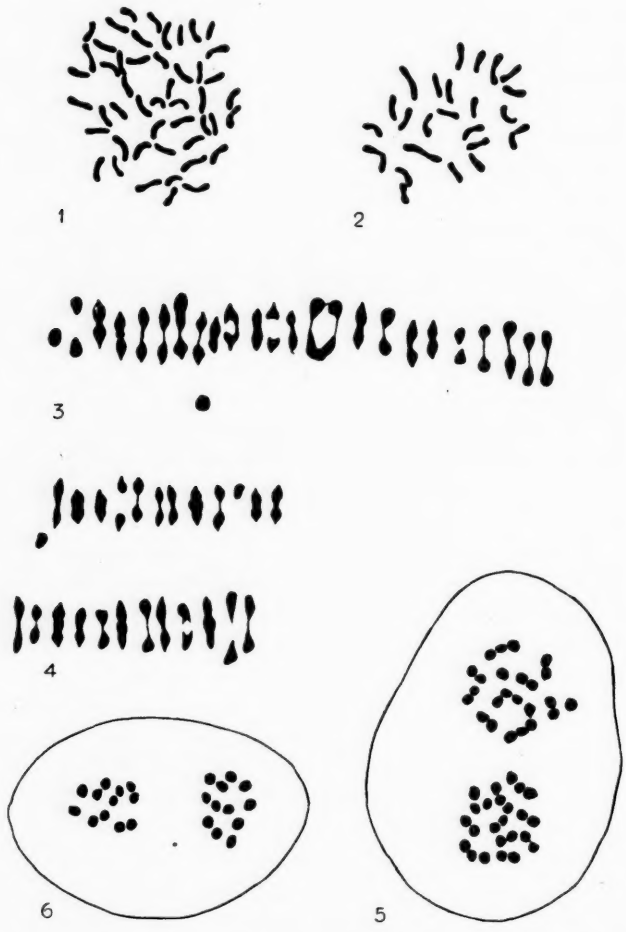
NOTES ON A HAPLOID POTATO HYBRID

BY *ROBERT LAMM*
ALNARP, ÅKARP, SWEDEN

IN the summer of 1936 the author observed a pair of twin seedlings in the progeny of a tetraploid F_1 hybrid between triploid *Solanum chaucha* and tetraploid *Solanum tuberosum* (LAMM, 1937; MÜNTZING, 1937). One of the two twin plants had the normal tetraploid chromosome number 48, the other twin plant had the gametic chromosome number 24 (Figs. 1 and 2). In the progeny of pure *Solanum andigenum* a pair of twins was also observed, but in this case both plants had 48 chromosomes. The occurrence of such twins may be associated with poly-embrony, which has been observed by several investigators in potato (YOUNG, 1922; KAUSCHE, 1937; LAMM, 1937). It is also possible that the occurrence of twins in potato, as in *Gossypium* (HARLAND, 1936), is typical of certain species and hybrids.

As a seedling, the haploid twin plant was exceedingly weak and did not flower but set a well developed tuber. In the following summer this tuber produced a much more vigorous plant, which also flowered. It has therefore been possible to study the reduction division in both twin plants. On the whole the chromosome pairing in both the 48-chromosome twin plant and in the likewise 48-chromosome F_1 hybrid took place in the same manner as in *Solanum tuberosum*. In addition to bivalents, quadrivalents and a remarkably high frequency of univalents and trivalents were observed (Fig. 3, Table 1). In tetraploid tomato trivalents are rare (UPCOTT, 1935), and in a tetraploid wild potato, *Solanum acaule*, PROPACH (1937) states that only true bivalent pairing occurs.

Of great interest are the pairing conditions observed in the poly-haploid 24-chromosome twin plant (Fig. 4, Table 1). In this plant 12 bivalents were observed in the majority of pollen mother cells at metaphase I, and many of these bivalents were joined by two chiasmata. The chiasma frequency, however, appears to be lower than in the normal diploid potato, of which the author has investigated closely related species. In both twin plants the homotypic division occurred quite normally (Figs. 5 and 6). In spite of the relatively regular reduction division the poly-haploid plant was strikingly pollen sterile.



Figs. 1—2. Somatic plates of the tetraploid and the poly-haploid twin plants. Fig. 1, $2n = 48$; Fig. 2, $2n = 24$. — Fig. 3. Complete nuclei of the tetraploid twin plant at first metaphase in side view with two univalents, twenty-one bivalents and one quadrivalent. — Fig. 4. Two complete nuclei of the poly-haploid twin plant at first metaphase in side view. — Figs. 5—6. Polar views of the second metaphase of the tetraploid and poly-haploid twin plant showing, in addition to secondary association, a regular distribution of the chromosomes. — The technique used was smearing, fixing in highly diluted Navashin and staining with gentian violet. — × 2,500.

TABLE 1. *Comparison of chiasma frequencies in the tetraploid and the poly-haploid twin plant. Of each plant twenty-five nuclei at first metaphase.*

Somatic chrosmosome number	Univalents	Bivalents		Trivalents		Quadri-valents		No. of ½-Xta per chromosome
		1 Xta	2 Xta	2 Xta	3 Xta	3 Xta	4 Xta	
24	16	218	74	—	—	—	—	1,22
48	68	306	117	40	2	25	15	1,27

The tetraploid plant had 50 per cent. good pollen, as compared with 9 per cent. in the haploid twin plant.

The pairing behaviour of the poly-haploid twin plant suggests a high degree of homology between the four genomes in the tetraploid F_1 hybrid. To draw any conclusions from the pairing conditions as to the nature of polyploidy is a difficult matter. DARLINGTON (1937) has described so-called differential pairing in diploid and tetraploid *Primula Kewensis*, a phenomenon which should also be present here.

TABLE 2. *Comparison between the two twin plants as to the thickness and length-breadth index of the apical leaves, size of the stomata and diameter of the pollen grains.*

	Somatic chromosome number	n	M ± m	v
Thickness of the leaves (mm.)	24	15	0,35 ± 0,018	20,3
	48	15	0,45 ± 0,020	17,6
Length-breadth index of the leaves	24	15	2,04 ± 0,039	7,5
	48	15	1,39 ± 0,033	9,1
Size of the stomata (μ)	24	50	14,86 ± 0,386	18,4
	48	50	22,65 ± 0,370	11,6
Diameter of the pollen grains (μ)	24	50	21,91 ± 0,246	7,9
	48	50	24,75 ± 0,255	7,3

Some morphological and anatomical examinations, the results of which will be briefly mentioned below, have also been made of the two twin plants. Tubers of the two twin plants were planted in April 1937. Cultivation was made in a greenhouse. Right from the beginning the tetraploid plant developed quite normally. In the poly-haploid plant, on the other hand, growth was at first very slow and it was not until

the weather became warmer that shoots begun to appear. Towards the end of the vegetative period both the twin plants had reached the same height, but the robust appearance of the tetraploid plant was in striking contrast to the slender form of the haploid plant. The two twin plants were most easily distinguishable by the shape of the leaves (Fig. 7). In the poly-haploid plant, as in normal diploids, the leaves were more

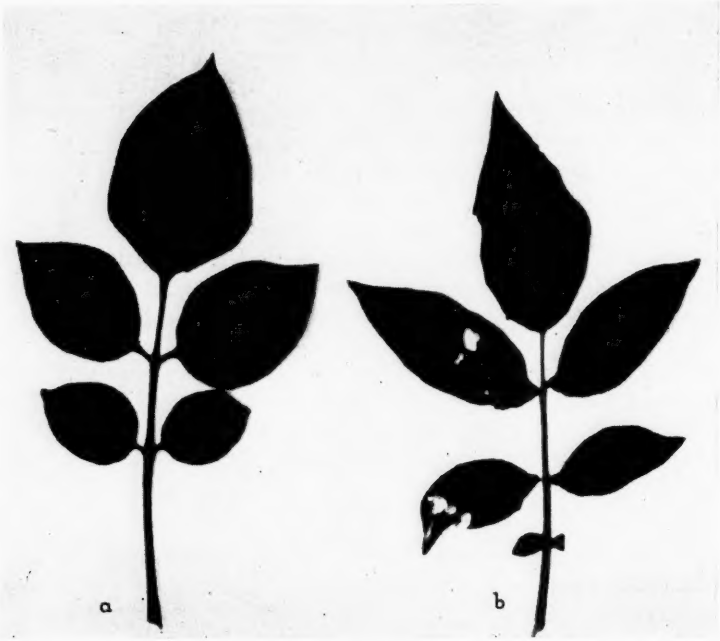


Fig. 7. Leaves of the tetraploid (*a*) and poly-haploid (*b*) twin plant.

or less tapering, thin and light green in colour. The leaves of the tetraploid plant were thick and wide, and dark green in colour. Measurements of the thickness of the leaves and the length-breadth index were carried out. The results are shown in Table 2, which also contains data of the size of the pollen grains and the stomata.

In respect to the size of the pollen grains, the poly-haploid twin plant agreed with normal diploids. The size of the pollen grains of a closely related species, *Solanum stenotonum*, was examined by the author at the same time. The size of the pollen grains of the tetraploid twin plant was that characteristic of tetraploid *Solanum tuberosum*.

The length of the stomata was also studied. Five leaves of each twin plant were taken, 10 stomata being measured in each leaf. As expected, the stomata of the tetraploid plant were much larger than those of the poly-haploid plant. The D/m value for both coefficients of variation, which refer to the length of the stomata, amounts to 2,80. The partial modification in this character was greater in the twin plant with the lower chromosome number. In measurements of stomata carried out by NISSEN (1937) on twin plants of grasses contrary results were obtained. FABERGÉ (1936), who investigated the partial modification of plant and fruit weight in diploid and tetraploid tomatoes, has, on the other hand, shown that this modification was least in tomatoes having the higher chromosome number. These interesting questions are worth further investigation. The differences between the other pairs of variation coefficients given in Table 2 are not statistically significant.

The present investigation was carried out at the Cyto-Genetic Department of the Swedish Seed Association, Svalöf, and to the Principal of that department, Professor A. MÜNTZING, the author wishes to express his thanks for the facilities so generously afforded him.

SUMMARY.

1. In the progeny of a tetraploid *Solanum chaucha* × *S. tuberosum* hybrid was observed a twin pair of seedlings, one of which was a tetraploid and the other a poly-haploid.

2. In the tetraploid 48-chromosome twin plant the reduction division occurred in the same manner as in tetraploid *Solanum tuberosum*. In the 24-chromosome poly-haploid twin plant 12 bivalents were observed in the majority of pollen mother cells at metaphase I.

3. Comparative measurements of the thickness and shape of the leaves, the diameter of the pollen grains and the length of the stomata cells were carried out on both twin plants.

Alnarp, January, 1938.

LITERATURE CITED.

1. DARLINGTON, C. D. 1937. Recent advances in cytology. Second Edition. — Churchill Ltd., London.
2. FABERGÉ, A. C. 1936. The physiological consequences of polyploidy. — Journ. of Genet., Vol. XXXIII, No. 3.

3. HARLAND, S. C. 1936. Haploids in polyembryonic seeds of Sea Island Cotton. — Journ. of Hered., Vol. 27, No. 6.
4. KAUSCHE, G. A. v. 1937. Über einige Anomalien in der Kartoffelblüte. — Zeitschr. f. Pflanzenkrankheiten, 47. Jahrg., Heft 3.
5. LAMM, R. 1937. A contribution to the embryology of the potato. — Svensk Bot. Tidskrift, Bd. 31.
6. MÜNTZING, A. 1937. Polyploidy from twin seedlings. — Cytologia, FUJII Jubilee Volume.
7. NISSEN, Ö. 1937. Spalteåpningenes störrelse hos tvillingplanter med ulike kromosomtall. — Botaniska Notiser.
8. PROPACH, H. 1937. Cytogenetische Untersuchungen in der Gattung *Solanum*, Sect. *Tuberarium*. II. Triploide und tetraploide Artbastarde. — Zeitschr. f. ind. Abst.- u. Vererb.-lehre, Bd. LXXII, Heft. 3/4.
9. UPCOTT, M. 1935. The cytology of triploid and tetraploid *Lycopersicum esculentum*. — Journ. of Genet., Vol. XXXI, No. 1.
10. YOUNG, W. J. 1922. Potato ovules with two embryo sacs. — Amer. Journ. of Bot., Vol. IX, No. 5.

CHROMOSOMENZAHLEN FINNLÄNDISCHER LEPIDOPTEREN

I. RHOPALOCERA

VON *HARRY FEDERLEY*
HELSINGFORS, FINNLAND

EINLEITUNG.

SYSTEMATISCHE Untersuchungen über Chromosomenzahlen gewisser Gattungen, Familien oder Ordnungen im Tierreich gibt es verhältnismässig wenige, wogegen die Botaniker auf eine stattliche Reihe solcher Untersuchungen aus dem Pflanzenreich hinweisen können. Das botanische Chromosomenmaterial ist ausserdem aus sehr verschiedenen Gegenden unserer Erde zusammengebracht, aus den hocharktischen sowie aus den heissesten und dürrsten Gebieten, und hat deshalb interessante Beziehungen zwischen Chromosomenzahlen und geographischen Verhältnissen zutage gebracht. Die verschiedenen Chromosomenzahlen der Arten einer Gattung scheinen uns auch die Möglichkeit zu bieten, gewissen ökologischen Problemen näher zu treten. In gewissen Fällen haben die Chromosomenzahlen uns überdies gestattet, einen tieferen Einblick in die phylogenetischen Beziehungen zwischen den Arten zu erhalten.

Die in zahlreichen Pflanzengattungen festgestellte Polyploidie und das nicht seltene Vorkommen schöner Reihen von Chromosomenzahlen, die eine lange arithmetische Serie bilden, kontrastieren scharf gegen die Verhältnisse in anderen Gattungen und Familien des Pflanzenreichs, in denen keine solche Gesetzmässigkeit vorkommt. Offenbar sind die Chromosomenzahlen in diesen beiden Gruppen in ganz verschiedener Weise entstanden. Die im Tierreich untersuchten Gattungen gehören fast alle zum späteren Typus, bei dem keine Gesetzmässigkeit in den Zahlenreihen festgestellt werden kann. Nur ganz selten findet man bei Tieren polyploide Arten. Unter diesen dürften die Formen *bivalens* und *univalens* von *Ascaris megalocephala* die bekanntesten sein. Was speziell die Lepidopteren anbetrifft, so kommen zwar Gattungen vor, in denen die Chromosomenzahlen als Multipeln einer gemeinsamen Grundzahl aufgefasst werden können. Es ist jedoch so gut wie sicher, dass sie nicht wie bei den Pflanzen infolge einer Kreuzung mit darauf

folgender Chromosomenverdoppelung entstanden sind. Zwar kommen Verdoppelungen des Chromosomensatzes in den Gameten zahlreicher Lepidopterenarten vor, aber diese diploiden Gameten scheinen nicht imstande zu sein, mit den normalen haploiden Gameten einen lebensfähigen triploiden Organismus ins Leben zu rufen. Es ist also sehr unwahrscheinlich, dass unter den Lepidopteren neue Arten durch Chromosomenverdoppelungen entstanden sind, wie dies mit Sicherheit bei vielen Pflanzen der Fall gewesen ist.

In manch einer anderen Hinsicht sind dagegen die Chromosomenverhältnisse der Lepidopteren interessant und regen zu Untersuchungen an. Als ich die Chromosomenverhältnisse bei Lepidopterenbastarden erforschte, suchte ich nach Arten, die sich nicht nur kreuzen lassen, sondern auch in bezug auf die Chromosomengarnitur geeignet sind, rätselhafte zytologische und genetische Fragen aufzuklären. Hierbei bemerkte ich bald, dass sich ein näheres und planmässiges Studium der Chromosomenverhältnisse der Schmetterlinge überhaupt lohnen würde. So konnten einander sehr ähnliche Arten und Formen ganz verschiedene Chromosomenzahlen besitzen. Es konnten aber auch die Individuen einer Art, ja sogar einer Population, Verschiedenheiten in der Chromosomenzahl aufweisen. Als Beispiel für den erstgenannten Fall möchte ich die beiden einander sehr ähnlichen und vermutlich nahe verwandten *Cerura*-Arten *furcula* und *bifida* nennen. Diese Arten haben die haploiden Chromosomenzahlen 29 und 49 und lassen sich trotzdem sehr leicht kreuzen. Ein anderes ähnliches Beispiel bietet die verwandte Art *Dicranura vinula*. Die in Finnland und Deutschland vorkommenden Formen dieser Art, die im männlichen Geschlecht auffallende Unterschiede zeigen, besitzen beide die haploide Chromosomenzahl 21, wogegen die in Albanien lebende *vinula*-Rasse 20 Chromosomen hat. Die als eine besondere Varietät unter dem Namen *delavoiei* beschriebene, in Marocko fliegende Form hat dagegen in den Oozyten 31 Chromosomen. Dabei lassen sich alle vier Formen in allen Kombinationen miteinander leicht kreuzen, und die Eier ergeben fast alle Raupen. Eine andere auffallende Erscheinung ist in diesem Zusammenhang erwähnenswert. Sie beweist nämlich klar, dass die Chromosomenzahl nicht etwas so starres und unveränderliches ist, wie oft angenommen wird. Wenn die in Finnland und Deutschland fliegenden *vinula*-Formen miteinander gekreuzt werden, so entsteht ein Bastard, der sowohl in den Spermatozyten als auch in den Oozyten in der Regel bloss 20 Chromosomen enthält. Es haben sich also als Folge der Kreuzung zwei Chromosomen der Elternarten im Bastard mitein-

ander vereinigt. Dies kann man in einigen Spermatozyten I andeutungsweise sehen, kommt jedoch klar in den Spermatozyten II zum Vorschein; diese können nämlich bisweilen 21 Chromosomen haben. Wir sehen also in diesem Fall einen Beweis für die Richtigkeit der Ansicht vieler Genetiker, dass auch das Verhalten der Chromosomen sowie die Chromosomenzahl von Genen reguliert wird (FEDERLEY, 1937).

Als ein Beispiel für solche Fälle, in denen zwei verschiedene Chromosomenzahlen in einer Population vorkommen, möchte ich *Leptidia sinapis* anführen. Bei dieser Art weist das Männchen die haploiden Chromosomenzahlen 26 und 27 auf, und als Seltenheit sogar 28. Dass es sich hier um eine Fusion zweier Chromosomen, resp. einer Fragmentierung eines Chromosoms handelt, geht deutlich daraus hervor, dass das Männchen mit 26 Chromosomen zwei lange Chromosomen, dasjenige mit 27 nur ein solches besitzt, und dass bei diesem letztgenannten als Seltenheit Spermatozyten mit 28 Chromosomen gefunden werden, die überhaupt keine langen Chromosomen aufweisen. Die langen Chromosomen entsprechen offenbar zwei kurzen. Es ist also klar, dass die Chromosomenzahl, d. h. die Verteilung der Gene auf eine bestimmte Anzahl Chromosomen, wie alle äusseren Merkmale überhaupt, nur ein phänotypischer Charakter ist, der sowohl von Genen als von der Umwelt determiniert wird.

Auch *Gonepteryx rhamni* tritt im männlichen Geschlecht in zwei verschiedenen Typen auf, in solchen mit 31 und solchen mit 32 Chromosomen, hier aber kommt die Fusion, resp. Fragmentierung nicht so klar zum Vorschein.

Eine andere überraschende Tatsache ist, dass die Chromosomenzahl in den beiden Geschlechtern einer Art eine verschiedene sein kann, wie es schon SEILER und HANIEL bei *Lymantria monacha* nachgewiesen haben. So besitzen z. B. die drei *Argynnis*-Arten *niobe*, *adippe* und *paphia* in den Spermatozyten I und II 29 Chromosomen, während die Oozyten I der genannten Arten nur 28 Chromosomen haben, worunter aber ein sehr langes. Ob es sich hier um eine Folgeerscheinung der Digametie im weiblichen Geschlecht handelt, habe ich leider nicht untersuchen können. Die Annahme einer Fusion, resp. einer Fragmentierung scheint jedoch hier am nächsten zu liegen.

Die zuerst von SEILER (1914) entdeckte und von anderen später bestätigte Digametie im weiblichen Geschlecht der Schmetterlinge war selbstverständlich auch eine Anregung, die Gametogenese zahlreicherer Lepidopterenarten kennen zu lernen. Leider bin ich in dieser Beziehung sehr enttäuscht geworden, denn die morphologisch nachweisbaren Fälle

von Digametie scheinen sehr selten zu sein. Zwar eignen sich die Tagschmetterlinge sehr wenig für solche Untersuchungen, da sie ihre Eier nicht leicht in der Gefangenschaft ablegen, ich habe indessen auch Vertreter verschiedener anderer Familien untersucht, ohne einen klaren und eindeutigen Fall finden zu können.

Die eigenartige Chromatinelimination während der ersten Reifeteilung in der Oogenese schien uns ebenfalls einer näheren Untersuchung wert zu sein, zumal die erste Reifeteilung bei vielen Arten vollständig wie eine Dreiteilung der Chromosomen aussieht. Da jedoch eine Untersuchung der Oogenese bei den Tagschmetterlingen grosse Schwierigkeiten bereitet, wird die Eliminationsfrage hier nur gestreift.

Schliesslich konnte SEILER (1925) eine Verschiedenheit der Chromosomenzahl bei verschiedenen geographischen Rassen von *Phragmatobia fuliginosa* nachweisen, wobei er die Elbe als die Grenze zwischen den Rassen mit 28 und 29 Chromosomen feststellte. Es schien deshalb wünschenswert, dass Individuen derselben Art aus verschiedenen Gegenden des Verbreitungsgebietes der Art untersucht würden, da Unterschiede in den Chromosomenverhältnissen bei den geographischen Rassen durchaus nicht ausgeschlossen sind. Diese Vermutung hat sich auch als berechtigt erwiesen, und es scheint, als ob solche Untersuchungen, in grösserem Massstabe ausgeführt, dazu beitragen könnten, deszendenztheoretische Fragen aufzuklären.

Die angeführten Tatsachen und Gesichtspunkte sprachen also dafür, die Chromosomenverhältnisse bei den Schmetterlingen einem planmässigen, systematischen Studium zu unterwerfen, wobei aber nicht nur die Spermatogenese, sondern vor allem auch die weit interessantere, wenn auch gleichzeitig viel mühsamer erforschte Oogenese Gegenstand der Untersuchung werden sollte. Es sind ja bis jetzt nur verhältnismässig wenige Arten in bezug auf ihre Chromosomenverhältnisse in beiden Geschlechtern untersucht worden. Dieser Mangel ist zwar begreiflich, da die Untersuchung der Oogenese sowohl bei Pflanzen als Tieren dem Zytologen ungeheuer grosse Schwierigkeiten bereitet und dazu sehr viel zeitraubender ist. Nichtsdestoweniger ist diese Lücke in unseren Kenntnissen sehr bedauerlich, denn die Spermatogenese gibt nicht nur ein unvollständiges Bild der Chromosomenverhältnisse der Art, sie kann auch ein falsches geben.

Meine Untersuchungen der Gametogenese wurden schon im Jahre 1912 angefangen und das Material ist im Laufe der Jahre allmählich

zusammengebracht und vorläufig untersucht worden. Während der Sommerperioden 1933—1937 habe ich planmässiger gearbeitet und mich ganz besonders bemüht, eine möglichst vollständige Sammlung von Präparaten der Gametogenese der Tagschmetterlinge anzulegen. Da man in der letzten Zeit auch anderswo angefangen hat, sich für die Chromosomenverhältnisse der Lepidopteren zu interessieren (BELIAJEFF, 1930; REGNART, 1930), habe ich mich dazu entschlossen, mein gesammeltes Material in systematischer Reihenfolge zu veröffentlichen, wobei ich mit den Tagschmetterlingen den Anfang mache. Von dieser systematisch gut begrenzten Gruppe besitze ich nämlich ein verhältnismässig reichhaltiges Material, indem mir nur einige der hochnordischen und allerseltensten südlichen Arten in Finnland fehlen. Ich hoffe, in Zukunft Gelegenheit zu finden, mein Material von den übrigen Gruppen zu vervollständigen und allmählich zu veröffentlichen.

Die Rhopaloceren sind für eine Untersuchung der Chromosomenverhältnisse in mancher Beziehung sehr dankbar. Sehr oft enthalten die neuausgeschlüpften Imagines noch beide Reifungsteilungen der Spermatogenese, und da die Oogenese hier, wie bei den meisten Lepidopteren, im Ovarium bis zur Metaphase — zuweilen sogar bis zur beginnenden Anaphase — der ersten Reifeteilung fortschreitet, so kann man auch einen Teil der Oogenese ohne besondere Zucht der Art erhalten. Hierzu kommt, dass die Ovarien sich in der Regel gut fixieren lassen und man alle die früheren Stadien, besonders die schönen Prophasen, in den Präparaten findet. Ein bedauerlicher Nachteil ist natürlich, dass die Reduktionsteilung nur mit grosser Mühe fixiert werden kann, da die Tagschmetterlinge ihre Eier erstens in der Regel nur einzeln auf die Nährpflanze ablegen und zweitens in der Gefangenschaft überhaupt schwer zur Ablage der Eier zu bewegen sind. Die Digametie kann aus diesen Gründen bei den Rhopaloceren kaum ohne ganz besondere Massregeln erforscht werden.

Als Fixiermittel habe ich in der letzten Zeit fast ausschliesslich das Gemisch von CARNOY (6 : 3 : 1) benutzt, da es nach meinen Erfahrungen, trotz all seiner Nachteile, dennoch das einzige Gemisch ist, auf das man sich verlassen kann, da es in die Eier gut und schnell eindringt und in der Regel sehr klare, wenn auch etwas schematische Bilder erzeugt. Selbstverständlich gibt es auch unter den Schmetterlingen Arten, für die es durchaus ungeeignet ist; diese gehören aber zu den Ausnahmen.

Es ist nicht meine Absicht, eine vollständige Beschreibung der

TABLLE 1. *Tabelle der Arten und ihrer Chromosomenzahlen.*

	Spermatogenese		Oogenese	
	Reifeteilung		Reifeteilung	
	I	II	I	II
Papilionidæ.				
Papilio machaon L.	30—33	30—33		
Parnassius apollo L.	30	30	30	
» *mnemosyne* L.			29	
Pieridæ.				
Aporia cratægi L.	25—26	25	25—26	
Pieris brassicæ L.	15	15	15	
» *rapæ* L.	26	26	26	
» *napi* L.	25	25	25	
Euchloe cardamines L.	31	31	30—32	
Leptidia sinapis L.	26—27	28	30—31?	
Colias palæno L.	31—32	31—32	31	
» *hecla* LEF. v. *sulitelma* AURIV.			31	
Gonepteryx rhamni L.	31—32	31—32	31?	
Nymphalidæ.				
Nymphalinæ.				
Limenitis populi L.	30		30	
Pyrameis atalanta L.	31	31		
Vanessa urticæ L.	31	31		
» *antiopa* L.	31	31	31	
Polygonia C-album L.	31	31	31	
Melitæa iduna DALM.			31	
» *maturna* L.			31	
» *cinxia* L.			31	
» *athalia* ROTT.	31	31	31	
Argynnis aphirape HB. v. *ossianus* HBST.			28	
Argynnis selene SCHIFF.	30	30	30	
» *euphrosyne* L.	31	31	31	
» *pales* SCHIFF. v. *arsilache* ESP.		30	29—30	
» *freija* THNB.	31		31	
» *frigga* THNB.			31	
» *thore* HB. v. *scandinavica* RYGGE			30	
Argynnis ino ROTT.	12—13	12—13	13—14	
» *lathonia* L.	30	30	30	
» *aglaja* L.	29	29	29	
» *niobe* L.	29	29	28—29	

	Spermatogenese		Oogenese	
	Reifeteilung		Reifeteilung	
	I	II	I	II
Argynnis adippe L.	29	29	28	
» *paphia* L.	29	29	28	
Satyrinæ.				
Erebia medusa F. v. *polaris* STAUD.			11	
» *ligea* L.			29	
» *lappona* ESP.			28	
» *disa* THNB.			29	
Oeneis jutta HB.			32	
Satyrus semele L.	29	29	29	
Pararge ægeria L. v. *ægerides* STGR.	28		28	
» *hiera* F.		29	29	
» *mæra* L.	28	28	28	
Aphantopus hyperantus L.			29	
Epinephele jurtina L.	29		29	
Coenonympha iphis SCHIFF.			29	
» *tiphon* ROTT.			29	
» *pamphilus* L.	29		28, 29	
Lycænidæ.				
Callophrys rubi L.			23	
Zephyrus betulæ L.			16?	
Chrysophanus virgaureæ L.	24	24	24	
» *hippothoë* L.			24	
» *phlæas* L.	24	24	24	
Lycæna argus L.	23	23	23	
» *aggrognomon* BRGSTR.	24	24	24	
» *optilete* KNOCH.	24		24	
» *astrarche* BRGSTR.	23	23	24	
» *eumedon* ESP.			24	
» *icarus* ROTT.	23		22—23	
» *amandus* SCHN.	23		23	
» *semiargus* ROTT.			24	
» *arion* L.			23	
Cyaniris argiolus L.			25	
Hesperidæ.				
Adopæa lineola L.	29		29	
Augiades sylvanus ESP.	29	29	29	28, 29
Hesperia alveus HB.	24		24	
» *malvæ* L.			31	

Gametogenese zu geben, obwohl sie in mancher Hinsicht von grossem Interesse wäre. Ich hoffe, vielleicht einmal Zeit zu finden, eine solche vergleichende Gametogenese der Lepidopteren auszuarbeiten; vorläufig aber muss ich mich hauptsächlich auf die Zahlenverhältnisse beschränken. Zunächst gebe ich in tabellarischer Form (Tabelle 1) die Chromosomenzahlen der 67 von mir untersuchten Arten in der Spermato- und Oogenese, soweit ich sie habe feststellen können, und alsdann im Anschluss an die Tabelle eine Beschreibung der Chromosomenverhältnisse.

PAPILIONIDÆ.

Die drei in Finnland vorkommenden Arten war ich in der Lage untersuchen zu können.

Papilio machaon. — Für diese Art gibt REGNART die Chromosomenzahl 30 an; dieselbe Zahl soll nach ihm auch für *P. podalirius* bezeichnend sein. Beide Zahlen wurden in der ersten Reifeteilung der Spermatozyten festgestellt. In meinem aus dem Kirchspiel Helsinge stammenden Material kann zwar diese Zahl auch in den Spermatozyten gefunden werden, jedoch nur als Seltenheit. Die Normalzahl ist zweifelsohne *32*. Daneben können die Zahlen 31 und 33 auch in demselben Testis vorkommen, sind jedoch als aberrative Zahlen zu betrachten. Fig. 1 gibt zwei Spermatogonienplatten mit etwa 60 Chromosomen und Spermatozytenplatten I und II mit genau 32 Chromosomen wieder.

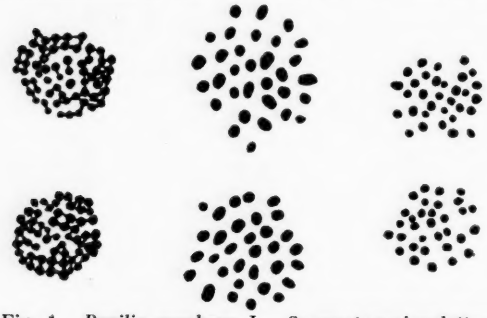


Fig. 1. *Papilio machaon* L. Spermatogonienplatten mit ca. 60 Chromosomen und Spermatozytenplatten I und II mit 32 Chromosomen; alle gezeichnet.

Über die Oogenese kann ich leider keine exakten Angaben machen, da sich der Kern mit dem Gemisch von CARNOY nicht fixieren lässt. Ich habe zwei grosse, an Eiern reiche Ovarien aus Imagines fixiert; trotzdem die Fixierung der Nähr- und Follikelzellen als ideal bezeichnet werden kann und dies auch mit dem Eiplasma nebst Einschlüssen der Fall ist, so erwies sich doch der Kern als ganz miserabel fixiert. Es müssen im Kern ganz besondere Verhältnisse walten, die die Fixierung erschweren oder fast unmöglich machen. Vermutlich ist die Kernmembran nur sehr wenig permeabel.

Die nordamerikanische Art *P. rutulus* soll nach MUNSON in den Spermatozyten 28 Chromosomen besitzen. MUNSON bildet jedoch Platten ab, in denen man deutlich 32 Chromosomen zählen kann, also dieselbe Zahl wie bei den finnländischen *machaon*-Individuen. KERNEWITZ hat in den Spermatogonien von *P. podalirius* 54—

58 Chromosomen feststellen können. Vielleicht kommen auch bei den *Papilio*-Arten verschiedene Zahlen bei verschiedenen Rassen oder sogar bei Individuen derselben Population vor, wie dies bei den Pieriden so häufig ist.

Parnassius apollo. — Das Material stammt aus den Kirchspielen Helsinge und Pojo.

Die Zahl *30* scheint beim Apollo in beiden Geschlechtern die alleinherrschende zu sein. In den zahlreichen von mir untersuchten Testes habe ich keine Abweichungen von dieser Zahl finden können, obgleich schöne Platten sowohl der ersten als zweiten Reifeteilung in Hülle und Fülle gefunden wurden. Nur ein einziges Weibchen habe ich untersucht, und nur in zwei Eiern konnte die Zahl *30* exakt festgestellt werden. Die Chromosomen sind bei dieser Art auffallend gross und zeigen nur ganz geringe Unterschiede in der Grösse.

Fig. 2 zeigt uns zwei Spermatozytenplatten I und eine Oozytenplatte I, alle gezeichnet.

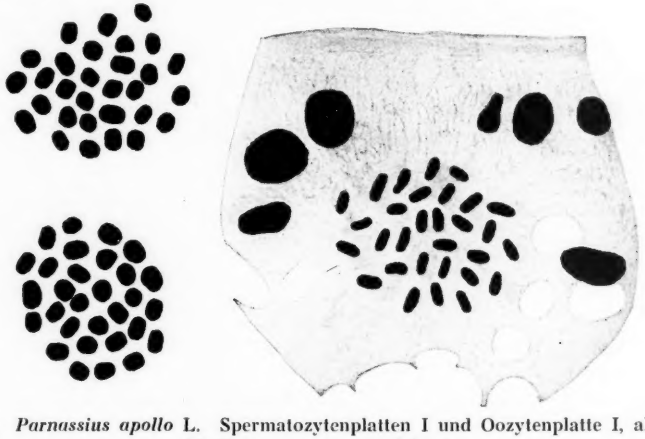


Fig. 2. *Parnassius apollo* L. Spermatozytenplatten I und Oozytenplatte I, alle mit 30 Chromosomen; gezeichnet.

P. mnemosyne. — Zwei Weibchen wurden von meinem Assistenten Herrn Mag. phil. ESKO SUOMALAINEN in der Nähe von Mariehamn, Åland, gefangen und fixiert. Beide zeigten dieselbe Zahl *29*, die in zwei ganzen Platten und vier auf zwei Schnitte verteilten Platten genau festgestellt werden konnte. Die Chromosomen sind untereinander ziemlich gleich gross.

PIERIDÆ.

Die Pieriden gehören in bezug auf die Zahlenverhältnisse der Chromosomen zu den interessantesten unter den von mir untersuchten Rhopaloceren. Es scheint, als ob die Familie sich in einer Periode der Veränderung der Chromosomenzahl befinden würde. In welcher Richtung diese Veränderung geschieht, ist natürlich nicht leicht zu entscheiden,

vieles deutet aber dennoch daraufhin, dass eine Fusion einzelner Chromosomen stattfindet und dass auf solche Weise eine Verminderung der Chromosomenzahl zustande gebracht wird.

Wie meine eigenen Untersuchungen und solche anderer Zytologen gezeigt haben, ist die Chromosomenzahl 31 in der Gametogenese der Schmetterlinge die allerhäufigste, und die meisten bekannten Zahlen liegen um diese Zahl herum, die Mehrzahl unter, verhältnismässig wenige über 31. Da nun die Zahlen 29—31 in fast allen Familien vorkommen, in den »primitiveren» sowie in den »höchst spezialisierten», erscheint es als berechtigt, diese Zahlen als ursprünglich zu betrachten; die Annahme, dass die verminderten Zahlen durch Fusion der Chromosomen entstanden sind, liegt sehr nahe. Allerdings muss zugegeben werden, dass die Verhältnisse bei den *Orgyia*- und den *Biston*-Arten für einen Prozess in der entgegengesetzten Richtung sprechen. Hier besitzen diejenigen Arten, deren Weibchen noch mehr oder weniger gut entwickelte Flügel haben, die geringeren Zahlen und die grössten Chromosomen, während die »höher differenzierten» Arten mit flügellosen und stark verkümmerten Weibchen eine grosse Zahl kleiner Chromosomen aufweisen. Hier ist die Hypothese, dass eine Fragmentierung der Chromosomen Hand in Hand mit der Differenzierung der Geschlechter stattgefunden habe, gut fundiert, wie CRETSCHMAR mit Recht hervorgehoben hat. Es ist jedoch nicht ausgeschlossen, dass die Entwicklung in den verschiedenen Familien verschiedene Wege eingeschlagen hat, und alles spricht dafür, dass wir bei den Rhopaloceren — wenigstens soweit mein Material beweiskräftig ist — eher einen Prozess der Fusion als der Fragmentierung der Chromosomen vor Augen haben. Dass ich bei *Dicranura vinula* direkt eine solche Fusion zweier Chromosomen als Folge einer Kreuzung zweier geographischer Rassen habe beobachten können, macht mich auch geneigt, eher eine Fusion anzunehmen.

Von den finnländischen Pieriden fehlen mir *Pieris daplidice* L. und die drei seltenen *Colias*-Arten *nastes* B., *hyale* L. und *edusa* F.

Aporia crataegi. — BELIAJEFF und KERNEWITZ geben beide die Zahl 25 für die Spermatozyten an.

Mein Material stammt aus zwei verschiedenen Kirchspielen in Südfinnland, das eine aus Pojo westlich, das andere aus Pernå östlich von Helsingfors. Die beiden Kirchspiele sind ungefähr 140 Kilometer voneinander entfernt. Ich gebe hier das Resultat meiner Zählungen an zwei Testes wieder.

Chromosomenzahl	25	26	27	28
Anzahl der Spermatozyten, Pojo	31	—	—	—
» » » Pernå	6	19	1	2

Von den Platten der Fig. 3 stammen die mit 25 Chromosomen aus Pojo, die mit 26 aus Pernå. Leider kommt in der letzterwähnten das 26. Chromosom nicht deutlich zum Vorschein. Es liegt links (9 Uhr) und ist nur durch einen Schatten angedeutet.

In der Oogenese kommen Platten vor, in denen man, wie die abgebildete Platte

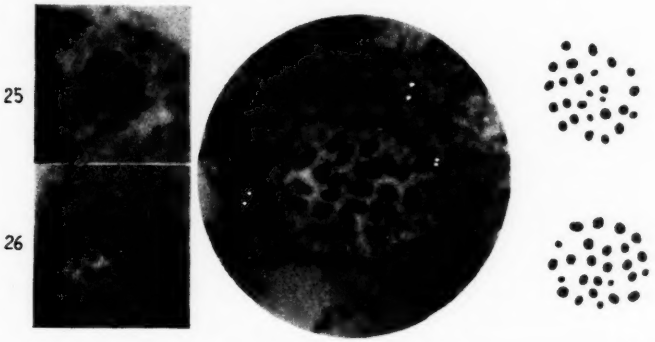


Fig. 3. *Aporia crataegi* L. Links photographierte Spermatozytenplatten I mit 25 und 26 Chromosomen, rechts gezeichnete mit 26; in der Mitte eine Oozytenplatte I mit 25 Chromosomen.

beweist, deutlich und einwandfrei 25 Chromosomen zählen kann, aber auch solche, in denen man exakt die Zahl 26 feststellen kann, und schliesslich auch Platten, wo es Geschmacksache ist, ob man 25 oder 26 als die Zahl angeben will. Die untersuchten Weibchen stammten beide aus Pernå, wo das Männchen ja auch eine Tendenz zur Fusion und gleichzeitig Fragmentierung zeigte.

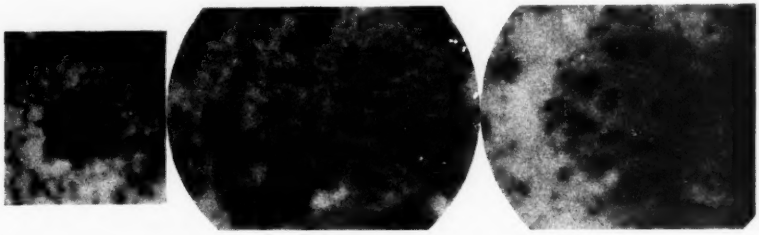


Fig. 4. *Pieris brassicæ* L. Spermatozytenplatte I, Prometaphase und Metaphase der ersten Reifeteilung im Ei. 15 Chromosomen.

Pieris brassicæ. — Die einzige beobachtete Zahl ist hier *15*. In 30 Oozytenplatten und in noch weit zahlreicheren Spermatozytenplatten I und II konnte diese für die Rhopaloceren kleine Zahl festgestellt werden. Siehe Fig. 4.

Die Photographien zeigen eine Spermatozytenplatte I, in der die beträchtliche Grösse der Chromosomen im Vergleich zu den zwei folgenden Arten auffällt, eine

Prometaphase der Oozyte I mit langen Chromosomen und Nukleolenresten und eine späte Metaphase mit stark verkürzten Chromosomen.

Bei *brassicæ* hat vermutlich die Fusionstendenz schon ihr Höchstmass erreicht, da andere Zahlen als 15 überhaupt nicht mehr gefunden werden. Auch BELIAJEFF und DONCASTER haben nur diese Zahl beobachtet. Dagegen gibt HENKING für das Weibchen die Zahl 14 und für das Männchen 14—15 an. Ob tatsächlich eine noch weiter gehende Fusion der Chromosomen in seinem Material zum Vorschein kam, ist schwer zu entscheiden.

Fig. 5. *Pieris rapæ* L. Spermatozytenplatte I mit 26 Chromosomen.

DONCASTER gibt an, dass in den von ihm untersuchten Spermatozytenplatten 3—4 Chromosomen durch ihre geringe Grösse auffallen. Auch in meinem Material kommen 3—4 kleinere Chromosomen vor, aber der Grössenunterschied ist, nach den Abbildungen von DONCASTER zu urteilen, bei den finnländischen Tieren weit weniger ausgesprochen.

B. rapæ. — BELIAJEFF hat in 20 Spermatozyten von 4 Individuen 25 Chromosomen gezählt.

Zu meiner Verfügung standen nur ein Männchen und ein Weibchen, letzteres aus Helsingfors. In 11 Spermatozytenplatten I und II und in 25 Oozytenplatten habe ich die Zahl *26* ganz sicher feststellen können. Fig. 5 gibt eine Spermatozytenplatte I wieder.

Es liegt also kein Zweifel vor, dass in Russland in der Gegend von Moskau, wo BELIAJEFF sein Material sammelte, eine *rapæ*-Rasse mit 25 Chromosomen lebt, wogegen die in Finnland fliegenden Individuen 26 Chromosomen besitzen, unter diesen ein besonders kleines.

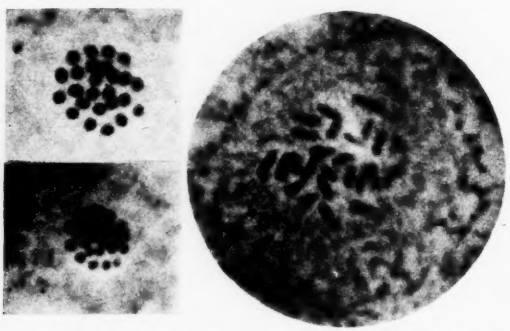


Fig. 6. *Pieris napi* L. Spermatozytenplatten I und II sowie Oozytenplatte I, alle mit 25 Chromosomen.

P. napi. — Nach HENKING soll diese Art 25 Chromosomen haben.

In 19 Spermatozyten I und II von vier Männchen und in 6 Oozyten I eines Weibchens habe auch ich 25 Chromosomen gezählt. (Fig. 6.)

Euchloe cardamines. — Nur bei einem Imagomännchen ist es mir gelungen, Reifeteilungen zu finden. In 7 Spermatozyten I und II konnten mit Sicherheit *31* Chromosomen gezählt werden, in einer 30.

In 3 Oozyten eines Weibchens war die Zahl sicher *30*, in einer vierten dagegen *32*. Diese äusserst klare Platte, in der alle Chromosomen in einer Ebene liegen, ist in Fig. 7 abgebildet, und man wird sich auf Grund derselben leicht überzeugen, dass die Zahl der Chromosomen tatsächlich 32 ist; die beiden untersten Flecke, von denen der eine wie ein kleines Chromosom aussieht, sind Nukleolenreste. Das Zählen der Chromosomen in den Oozyten dieser Art wird dadurch sehr erschwert, dass die Nukleolen so spät verschwinden.

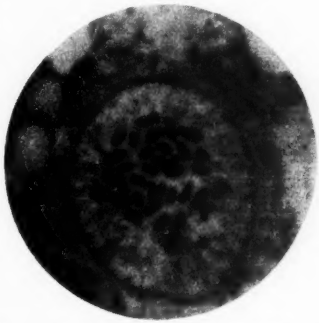


Fig. 7. *Euchloe cardamines* L. Oozytenplatte I mit 32 Chromosomen.

Leptidia sinapis. — Diese Art gehört zu den interessantesten unter den von mir untersuchten Arten. Wie schon in der Einleitung erwähnt wurde, findet man vom Männchen zwei verschiedene Typen, solche mit *26* und solche mit *27* Chromosomen. Ausnahmsweise kommen auch Platten mit 28 Chromosomen vor. Wie Fig. 8 zeigt, haben die beiden Platten mit 26 Chromosomen zwei lange Chromosomen. Wir

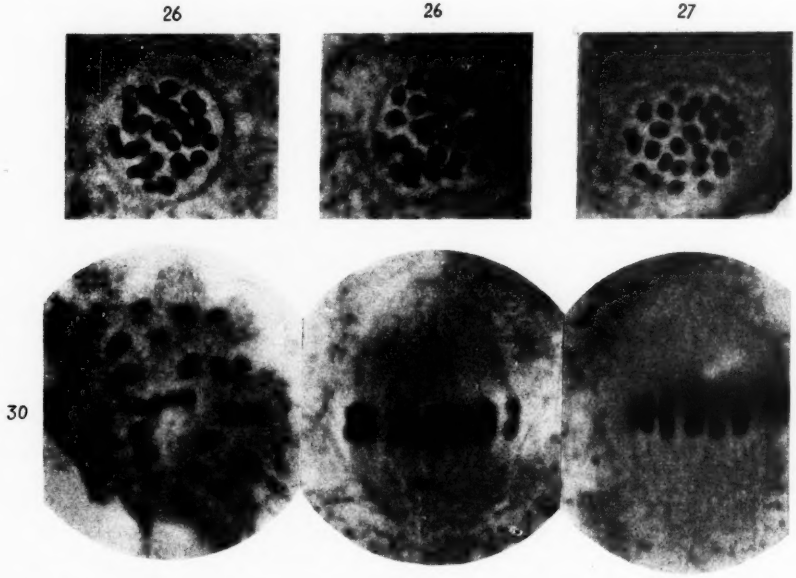


Fig. 8. *Leptidia sinapis* L. Spermatozytenplatten I, zwei mit 26 und eine (rechts) mit 27 Chromosomen. Oozytenplatte I mit ca. 30 Chromosomen. Rechts eine normale Spindel mit bivalenten Chromosomen, in der Mitte eine mit »sekundärer Bindung» der Chromosomen, Kettenbildung.

erkennen sie in der Platte links an der Peripherie links unten (7 und 9 Uhr) und in der Platte in der Mitte im Zentrum und links (8 Uhr), das letzterwähnte etwas verwischt, weil es niedriger liegt. In der Platte rechts mit 27 Chromosomen gibt es nur ein langes, das links (9 Uhr) peripherisch liegt. In dem Männchen mit 26 Chromosomen wurde diese Zahl in 9 Spermatozyten I genau festgestellt, und alle Platten waren von demselben Typus wie die abgebildeten. Das andere Männchen besass in 24 Spermatozyten I 27 Chromosomen, unter diesen nur ein langes, und in drei Spermatozyten II 28 Chromosomen. In den letzterwähnten Platten kam kein langes Chromosom vor, und die Vermutung liegt nahe, dass das lange Chromosom in zwei zerlegt ist. Dieser Schluss scheint mir um so mehr berechtigt, als die in den Spermatozyten I des Bastards zwischen der deutschen und finnländischen *vinula*-Form assoziierten Chromosomen in den Spermatozyten II nicht selten wieder getrennt auftreten.

Das Studium der Oozyten macht grosse Schwierigkeiten, weil in der Oogenese dieser Art in der Metaphase eine Assoziation einiger Chromosomen, etwa deren fünf, in der Regel stattfindet. Diese Verbindung bivalenter Chromosomen erweckt den Eindruck einer »sekundären Paarung», wie sie häufig bei Pflanzen beschrieben worden ist. Dass sie wie bei den Pflanzen als ein Indizium einer Polyploidie aufgefasst werden könnte, scheint mir nicht wahrscheinlich. Ein Fixierungsartefakt stellen sie auch nicht dar. Worum es sich eigentlich handelt, darüber können nur zukünftige eingehendere Untersuchungen Bescheid geben.

Die Oozytenplatten sind an und für sich äusserst klar, und die einzelnen Chromosomen liegen weit voneinander entfernt, in allen Platten aber findet man eine Kette von verbundenen Chromosomen, in der es nicht möglich ist, die Zahl der Einzelchromosomen exakt festzustellen. In der abgebildeten Platte sehen wir in der Mitte eine solche Kette, und in der in der Mitte wiedergegebenen Spindel eine Reihe verbundener Chromosomen von der Seite. Die Spindel rechts zeigt uns die normalen bivalenten Chromosomen während der Metaphase. Die Schätzung der Zahl der teilnehmenden Chromosomen wird dadurch noch weiter erschwert, dass die Anaphase bald beginnt und die Chromosomen dann aus drei Kugeln bestehen, von denen die in der Mitte liegende das Eliminationschromatin ist. In der Kette mit den schief gestellten Chromosomen wird ein exaktes Zählen demzufolge unmöglich. Immerhin habe ich den Versuch gemacht, die Zahl ungefähr zu schätzen, wobei ich zu dem überraschenden Resultat gelangt bin, dass bei den vier von mir untersuchten Weibchen die Chromosomenzahl in der ersten Reifeteilung auf *30* geschätzt werden muss, eher 31 als unter 30. Die abgebildete Platte zeigt ja auch deutlich 25 freiliegende Chromosomen und dazu die Kette, in der vermutlich fünf Chromosomen vorhanden sind.

Colias palæno. — Von dieser Art habe ich 2 Männchen und 1 Weibchen aus Pernå untersucht. Ich gebe hier das Resultat der Zählung in den beiden Testes wieder.

Chromosomenzahl	31	32	33	34
Anzahl Spermatozyten, Testis I	4	11	—	—
» » » II	1	13	2	2

Die Zahl *32* scheint demnach die häufigste zu sein. Fig. 9 zeigt diese Zahl.

Beim Weibchen konnte ich nur in 3 Platten die Zahl ganz genau feststellen. Sie war in allen *31*. Unter den Chromosomen fällt eines von ihnen durch seine bedeutende Grösse auf. In Fig. 9 liegt es rechts an der Peripherie.

Im Sommer 1937 gelang es Herrn Mag. phil. A. Fr. Nordman ein Weibchen dieser Art in Utsjoki zu fangen. Der Fundort liegt unbedeutend südlicher als die 70. Breite. Mit grosser Spannung machte ich mich an die Untersuchung dieses hochnordischen Individuums. Es zeigte sich indessen, dass die Chromosomenzahl dieselbe ist wie bei den auf der 60. Breite gefangenen Exemplaren. In drei Oozytenplatten konnte ich nämlich die Chromosomenzahl *31* exakt feststellen und auch ein

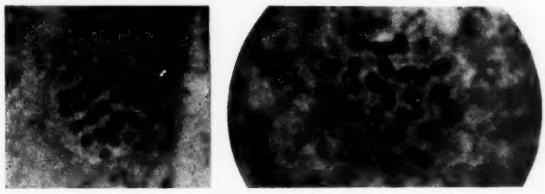


Fig. 9. *Colias palæno* L. Spermatozytenplatte I mit 32 Chromosomen, Oozytenplatte mit 31 Chromosomen.

grösseres Chromosom kommt vor. Es scheint demnach, als ob die *palæno*-Rassen sowohl im Süden als auch im hohen Norden Finnlands dieselbe Chromosomenzahl hätten.

C. hecla v. *sulitelma*. — Von dieser hochnordischen Art hat mir Mag. Nordman ein von ihm in Utsjoki gefangenes und fixiertes Individuum zur Verfügung gestellt. Auch für diese Art scheint die Chromosomenzahl *31* charakteristisch zu sein. In

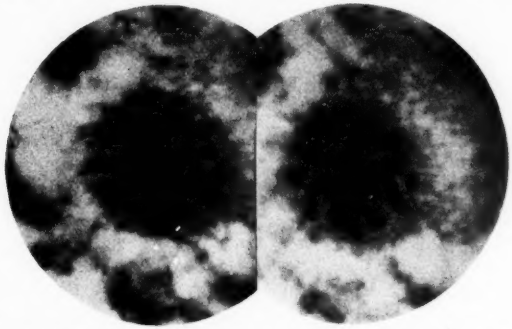


Fig. 10. *Colias hecla* Lef. v. *sulitelma* Auriv. Oozytenplatte I mit 31 Chromosomen in zwei Ebenen photographiert.

9 Oozytenplatten I konnte ich diese Zahl exakt zählen. Die Chromosomen sind durchschnittlich kleiner als bei *palæno*; die Grösse der einzelnen Chromosomen ist etwas verschieden, es kommt jedoch kein besonders grosses vor. Vergleich Fig. 10.

Gonepteryx rhamni. — Für diese Art gibt Kernewitz für das Männchen die haploide Zahl 31 an. In meinem Material kommt diese Zahl ebenfalls vor. Es scheint jedoch, als ob in Finnland zwei Typen von Männchen vorkämen, nämlich solche mit 31 und solche mit 32 Chromosomen. Ich gebe hier das Resultat einer Untersuchung der Testes von fünf Männchen wieder.

Chromosomenzahl	31	32
Anzahl Spermatozyten im Testis I	3	12
» » » » II	7	33
» » » » III	—	18
» » » » IV	11	—
» » » » V	6	—

Wie aus der Tabelle hervorgeht, enthalten die Testes IV und V lauter Spermatozyten mit *31* Chromosomen und der Testis III lauter solche mit *32*, während die Testes I und II beide Zahlen aufweisen, wobei die Zahl 32 allerdings stark über-

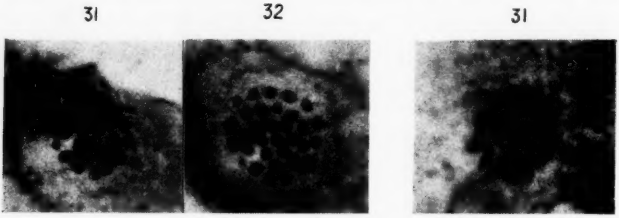


Fig. 11. *Gonepteryx rhamni* L. Spermatozytenplatten I mit 31 und 32 Chromosomen und Oozytenplatte mit ca. 31 Chromosomen.

wiegt. Diese kommt insgesamt in 63 Platten, die Zahl 31 nur in 27 Platten vor. Siehe Fig. 11.

Die Oozytenplatten sind verhältnismässig klein, und die Neigung der Chromosomen, Perlenketten zu bilden, scheint bei dieser Art besonders ausgesprochen zu sein. Dies erschwert die exakte Zählung der Chromosomen. Bei den zwei von mir untersuchten Weibchen habe ich in mehreren Platten *31* Chromosomen zählen können. In weniger klaren Platten schien die Zahl auch 30 und 32 zu sein, wobei aber diese Zahlen mit gewissem Vorbehalt angeführt seien.

NYMPHALIDÆ.

NYMPHALINÆ.

Limenitis populi. — Von dieser in Finnland ziemlich seltenen Art habe ich zwei Testes neuausgeschlüpfter Imagines und ein Ovar aus einem alten Weibchen untersucht. Nur der eine Testis enthielt noch einige Reifeteilungen, während der andere lauter apyrene Teilungen aufwies. Es gelang mir, in fünf Spermatozyten I sicher *30* Chromosomen zu zählen und in zwei etwa 29—30. In drei Oozytenplatten war es möglich, genau *30* Chromosomen nachzuweisen.

Die beiden tauglichen Exemplare verdanke ich meinem Assistenten Herrn Mag. phil. ESKO SUOMALAINEN, der sie in der Nähe der Stadt Borgå erbeutete.

Pyrameis atalanta. — Von dieser Art wurde mir ein fixierter Testis eines an der Zoologischen Station Tvärminne von Mag. SUOMALAINEN gefangenen, frisch ausgeschlüpften Imago zur Verfügung gestellt. Der Testis enthielt noch verhältnismässig viele Zysten mit Reifeteilungen, so dass ich in 10 Platten I und II sicher 31 Chromosomen zählen konnte. Die Platten sind kaum von denjenigen der folgenden drei Arten zu unterscheiden.

Vanessa urticæ. — BELIAJEFF hat beim Männchen 31 Chromosomen gezählt. In einem Testis einer Raupe fand auch ich 25 Spermatozyten mit *31* Chromosomen und nur eine mit 32. Fig. 12 gibt Platten beider Reifeteilungen wieder.

V. antiopa. — Für diese Art gibt STEVENS die Zahl 30 an. Ich habe sowohl Männchen als Weibchen aus Finnland untersucht und dabei gefunden, dass beide Geschlechter *31* Chromosomen besitzen. Da STEVENS ihr Material vermutlich aus Nordamerika, wo die Art vorkommt, erhalten hatte, scheint es wahrscheinlich, dass sich die geographischen Rassen der Art in bezug auf die Chromosomenzahl unterscheiden. STEVENS hebt hervor, dass eines der Chromosomen die übrigen an Grösse erheblich übertrifft, und die Abbildung bestätigt dies in schönster Weise. Es liegt also die Annahme nahe, dass bei der amerikanischen Rasse zwei Chromosomen miteinander vereinigt sind. Denn wie Fig. 13 von zwei Spermatozyten I finnländischer Falter zeigt, kommt bei diesen kein besonders grosses Chromosom vor.

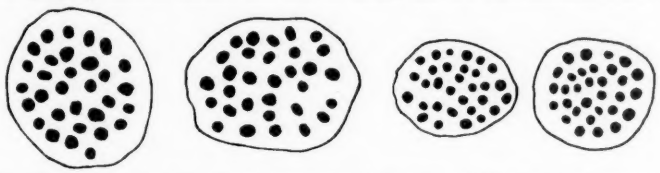


Fig. 12. *Vanessa urticæ* L. Spermatozytenplatten I und II mit 31 Chromosomen; gezeichnet.

Polygonia C-album. — KERNEWITZ und BELIAJEFF haben beim Männchen 31 Chromosomen gezählt. Die von mir untersuchten Individuen enthielten in beiden Geschlechtern gleichfalls *31* Chromosomen.

Melitæa iduna. — Mag. NORDMAN hat mir ein Ovarium dieser nur in Lappland fliegenden Art fixiert. Das Ovar enthielt zahlreiche Eier, und in sechs Oozytenplatten I, die in einem Schnitt lagen, konnte die Chromosomenzahl exakt als *31* festgestellt werden, und in weiteren drei Platten, die auf zwei Schnitte verteilt worden waren, kam dieselbe Zahl vor.

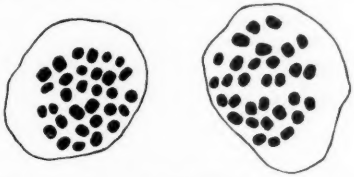


Fig. 13. *Vanessa antiopa* L. Spermatozytenplatten I mit 31 Chromosomen; gezeichnet.

M. maturna. — BELIAJEFF gibt für das Männchen 31 als die typische Chromosomenzahl an; die von mir gefangenen, neuausgeschlüpften Imagines enthielten lauter apyrene Reifeteilungen. Bei einem von Mag. SUOMALAINEN in der Nähe von Borgå gefangenen Weibchen konnte ich dagegen an zehn Oozytenplatten die Zahl *31* einwandfrei feststellen.

M. cinxia. — Die Ovarien der zwei Weibchen, die ich in der Lage war zu untersuchen, wurden auch von Mag. SUOMALAINEN gefangen und fixiert; sie stammten aus Åland, Mariehamn. In den Oozyten beider Ovarien konnten in zusammen 14 Fällen exakt *31* Chromosomen gezählt werden. Das eine Ovar enthielt ausserdem noch fünf vom Messer durchschnittene Platten, die sicher 31 Chromosomen besassen. Das andere hatte dagegen drei Platten mit 30 Chromosomen. Ob bei *cinxia* sowohl die Zahl 31 als auch die Zahl 30 tatsächlich vorkommt, wage ich nach

dem vorliegendem Material nicht zu entscheiden. In Fig. 14 ist eine Platte mit 31 Chromosomen photographiert.

M. athalia. — Auch diese Art besitzt in beiden Geschlechtern die Chromosomenzahl *31*. Wie Fig. 15 zeigt, sind die Chromosomen untereinander hinsichtlich der Grösse nicht erheblich verschieden, wie dies auch bei den anderen Arten der Fall ist.

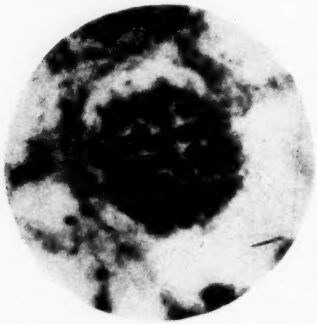


Fig. 14. *Melitæa cinxia* L. Oozytenplatte mit 31 Chromosomen.

Die Gattung *Argynnis* gehört zu den an Arten reichsten im Norden. Es ist mir gelungen von 14 Arten Material zu erhalten. Unter diesen befindet sich *A. ino*, die durch die geringe Zahl von nur 12—14 Chromosomen charakterisiert ist. Die Chromosomenzahlen der übrigen Arten liegen zwischen 28 und 31.

Argynnis aphirape v. *ossianus.* — Das Material dieser Art stammt aus der Umgebung von Borgå und wurde mir von Mag. SUOMALAINEN gesandt. Die jungen Männchen enthielten keine Reifeteilungen, weshalb ich nichts über die Chromosomenzahlen des männlichen Geschlechts mitteilen kann. Ein Ovarium besass dagegen zahlreiche Metaphasen I; in neun von diesen konnte ich mit Sicherheit exakt *28*

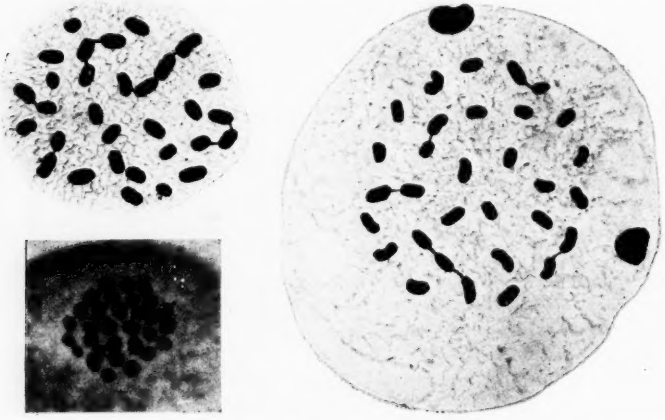


Fig. 15. *Melitæa athalia* ROTT. Spermatozytenplatte I, photographiert, gezeichnete Oozytenplatten I, alle mit 31 Chromosomen.

Chromosomen zählen. Fig. 16 zeigt deutlich diese Zahl sowie die geringen Grössenunterschiede der Chromosomen.

Arg. selene. — Das Männchen hat in beiden Reifeteilungen *30* Chromosomen. Fig. 17 stellt eine Platte der 2. Reifeteilung dar. Ein besonders grosses Chromosom in der Mitte der Platte fällt auf. Auch die Oozytenplatten I enthalten klar *30*

Chromosomen, worunter ein grosses. Es kommen jedoch auch Platten mit 29 Chromosomen vor.

Arg. euphrosyne. — In beiden Reifeteilungen weist das Männchen *31* Chromosomen auf, von denen keines durch besondere Grösse auffällt. Fig. 18 einer Spermatozyte II überzeugt uns hiervon. Das Weibchen zeigt gleichfalls *31* untereinander ziemlich gleichgrosse Chromosomen, wie die ungewöhnlich klare Fig. 18 beweist. Leider fehlt ein Chromosom in der Platte; es liegt im folgenden Schnitt.

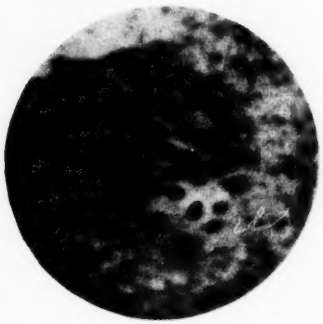


Fig. 16. *Argynnis aphirape* Hb. v. *ossianus* Hbst. Oozytenplatte I mit 28 Chromosomen.

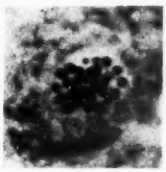


Fig. 17. *Argynnis selene* Schiff. Spermatozytenplatte II mit 30 Chromosomen.

Die Annahme, dass das grosse Chromosom bei *Arg. selene* zwei Chromosomen bei *euphrosyne* entspricht, liegt sehr nahe.

Arg. pales v. *arsilache.* — Die wenigen Platten der 2. Reifeteilung, die ich im Testis eines neuausgeschlüpften Männchens finden konnte, hatten alle deutlich *30* Chromosomen. Beim Weibchen war es dagegen möglich, mit Sicherheit zwei verschiedene Zahlen in den Metaphasen I nachzuweisen, nämlich *30* und *29*. Dazu kam noch eine Anzahl Platten, in denen es nicht möglich war zu entscheiden, ob die Zahl 30 oder 29 war. Die Art bildet vielleicht einen Übergang zu den Arten *niobe*, *adippe* und *paphia*, bei denen die Weibchen immer ein Chromosom weniger besitzen als die Männchen, d. h. beim Weibchen haben sich zwei Chromosomen vereinigt.

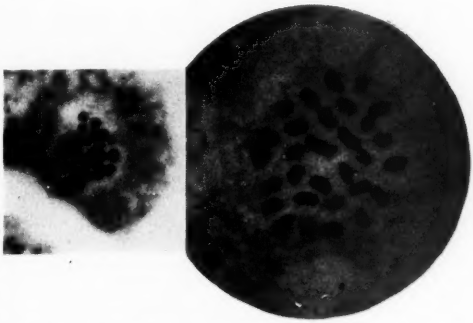


Fig. 18. *Argynnis euphrosyne* L. Spermatozytenplatte II und Oozytenplatte I, beide mit 31 Chromosomen. In der Oozyte fehlt ein Chromosom, das im folgenden Schnitt liegt.

Auch das Material dieser Art wurde von Mag. Suomalainen in der Nähe von Borgå eingesammelt und zu meiner Verfügung gestellt.

Arg. freija. — Das Material stammt aus der Umgebung von Helsingfors, wo die Art Ende Mai auf den Mooren nicht selten fliegt. Es wurde von Mag. SUOMALAINEN eingesammelt und fixiert.

Mehrere Testes neuausgeschlüpfter Imagines wurden von mir sorgfältig durchsucht, ohne dass es mir gelungen wäre, Reifeteilungen zu finden. Schliesslich fand ich dennoch eine einzige Spermatozyte I, in der es möglich war, *31* Chromosomen zu zählen. Offenbar findet die Spermatogenese schon in der jungen Puppe statt.

Die Ovarien zweier Weibchen habe ich genau untersucht und dabei 10 Oozyten I mit *31* Chromosomen in einer Platte entdeckt. Ausserdem fand ich noch vier auf zwei Schnitte verteilte Platten, in denen die Zahl 31 auch einwandfrei festgestellt werden konnte. Fig. 19 gibt eine in zwei Aufnahmen photographierte, etwas schräge Platte wieder. Wie die Photographie zeigt, sind die Chromosomen untereinander ziemlich gleich gross. Das scheinbar einheitliche grosse Chromosom

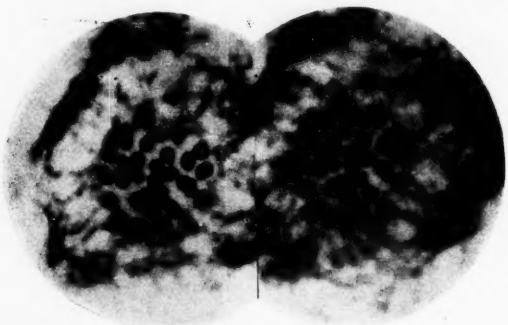


Fig. 19. *Argynnis freija* THUNB. Oozytenplatte I mit 31 Chromosomen in zwei Ebenen photographiert.

(4 Uhr) besteht aus zwei Chromosomen, die schräg untereinander liegen und auf dem Bilde verschmelzen.

Arg. polaris. — Von dieser hochnordischen Art fixierte mir Mag. NORDMAN ein Ovar, das leider keine vollständig reife Eier enthielt. Die Eier hatten schon ihre volle Grösse erreicht, jedoch ohne Reifeteilungen zu zeigen.

Arg. frigga. — Von dieser verhältnismässig seltenen Art habe ich durch die Güte des Herrn Oberlehrer Dr. ROLF KROGERUS zwei Weibchen erhalten, die er in Kivinebb in Ostfinnland erbeutet hatte. Leider kam die Sendung verzögert bei mir an, und die Weibchen waren tot. Da sie jedoch noch ganz weich waren, fixierte ich sie, wonach es sich zeigte, dass viele der Eier ganz gut fixiert waren und eine exakte Feststellung der Chromosomenzahl erlaubten.

Die Chromosomenzahl in den Oozyten I ist *31*. Unter den Chromosomen fällt ein kleines und schlankes Chromosom dadurch auf, dass es öfters in einer anderen Ebene als die übrigen liegt.

Arg. thore v. *scandinavica.* — Die zwei von mir untersuchten Ovarien wurden von Mag. NORDMAN in Haukilampi in Nordlappland fixiert. Beide enthielten zahlreiche Eier. Bei fünfzehn von ihnen gelang es mir, exakt *30* Chromosomen zu

zählen. Wie Fig. 20 zeigt, sind die Grössenunterschiede unter den Chromosomen nicht besonders gross.

Arg. ino. — Diese Art gehört zu den interessantesten, weil sie erstens eine so geringe Chromosomenzahl besitzt und zweitens verschiedene Zahlen aufweist.

In einem Testis habe ich in 23 Platten der 1. und 2. Reifeteilung *13* Chromosomen gezählt. Eine andere Zahl kam überhaupt nicht vor. In anderen Testes habe ich dagegen sowohl die Zahl *13* als *12* feststellen können. In den Platten mit 12 Chromosomen hatte ein Chromosom öfters die Form einer Acht, ein Zeichen

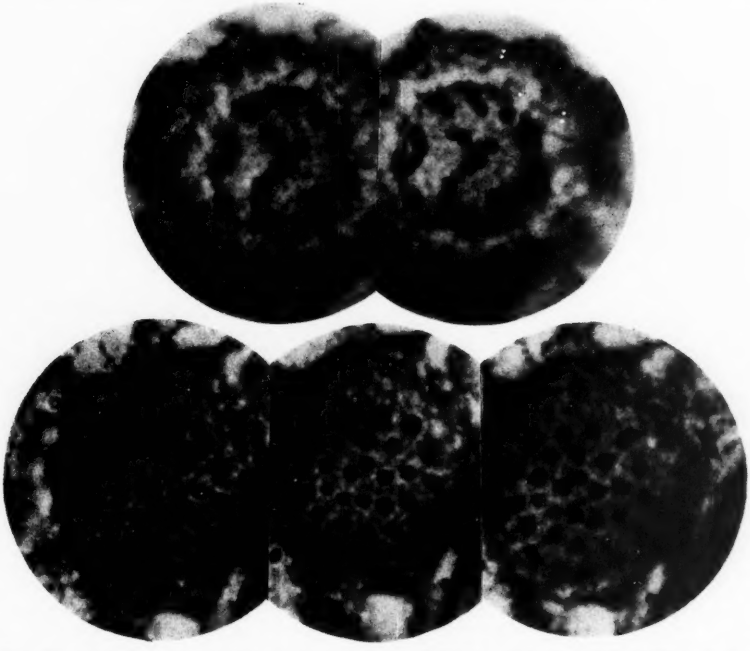


Fig. 20. *Argynnis thore* Hb. v. *scandinavica* Rygge. Zwei Oozytenplatten mit 30 Chromosomen in zwei resp. drei Ebenen photographiert. Die Chromosomen der oberen agglutiniert.

dafür, dass es eigentlich aus zwei Chromosomen zusammengesetzt ist. Beide Zahlen kommen in beiden Reifeteilungen vor, aber die Platten mit 13 scheinen häufiger zu sein als die mit 12 Chromosomen. Das Verhältnis war 34 zu 18; dazu kamen noch 7 Platten, in denen es Geschmacksache war, ob man die Zahl als 12 oder 13 angeben wollte. Fig. 21 zeigt uns eine sehr schöne und klare Platte I mit 12 Chromosomen und zwei Platten II mit 13.

In den Oozyten ist die Zahl *13* die häufigste; die Zahl 12 habe ich überhaupt nicht beobachtet. Dagegen habe ich einige Platten gefunden, in denen 14 Chromosomen mit grosser Wahrscheinlichkeit gezählt werden konnten. Fig. 21 zeigt uns eine Oozytenplatte mit 13 Chromosomen.

Wie die Abbildungen beweisen, sind die Chromosomen von erheblicher Grösse. *Arg. ino* bildet gewissermassen in bezug auf die Chromosomenverhältnisse eine Parallele zu *Pieris brassicæ*, die gleichfalls eine geringe Zahl grosser Chromosomen besitzt.

Arg. lathonia. — Beide Geschlechter enthalten in den Reifeteilungen *30* Chro-

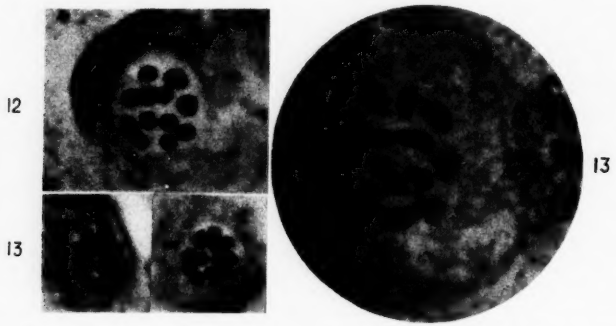


Fig. 21. *Argynnis ino* ROTT. Spermatozytenplatten: I mit 12 und II mit 13, Oozytenplatte I mit 13 Chromosomen.

mosomen. Sie sind von ziemlich gleichmässiger Grösse, in einigen Oozyten kann jedoch ein längeres Chromosom beobachtet werden. In Fig. 22 ist eine Oozytenplatte photographiert.

Arg. aglaja. — Das Männchen weist in beiden Reifeteilungen *29* Chromoso-

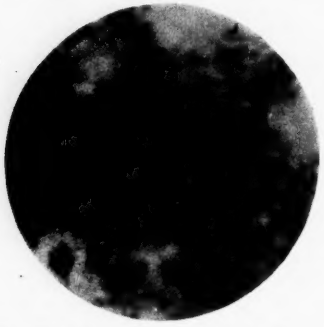


Fig. 22. *Argynnis lathonia* L. Oozytenplatte mit 30 Chromosomen.

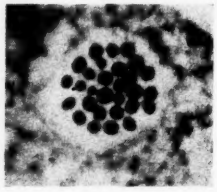


Fig. 23. *Argynnis aglaja* L. Spermatozytenplatte I mit 29 Chromosomen.

men auf. Siehe Fig. 23. Dieselbe Zahl wird auch in den Oozytenplatten I gefunden.

Arg. niobe. — Bei 4 Männchen habe ich in 44 Spermatozyten I und II 29 Chromosomen gezählt. Nur in einer einzigen Platte war die Anzahl 30.

Dagegen besitzt das Weibchen in der Regel in den Oozytenplatten I *28* Chromosomen und unter diesen ein auffallend grosses. In Fig. 24 liegt dieses grosse Chromosom in der Mitte der Platte. Oft zeigt es eine Einschnürung, die auf seine

zusammengesetzte Natur hinweist. Die Chromosomenzahl 28 habe ich bei einem Weibchen in 14 Platten genau feststellen können. Bei einem anderen Weibchen überwog die Zahl 28 ebenfalls, wobei aber auch einzelne Platten mit 29 Chromosomen vorkamen. In diesen Platten konnte kein grosses Chromosom entdeckt werden.

Fig. 24. *Argynnis niobe* L. Spermatozytenplatte I mit 29 Chromosomen, Oozytenplatte I in zwei Aufnahmen mit 28 Chromosomen.

Die untersuchten Weibchen stammten beide aus Ost-Nyland, Pernå, Sarvsalö, die vier Männchen dagegen aus West-Nyland, Pojo.

Arg. adippe. — Diese Art verhält sich genau so wie die vorige. Bei vier Männchen habe ich in 86 Spermatozytenplatten I und II ganz exakt 29 Chromosomen gezählt; in einer Platte II nur 27.

Beim Weibchen ist dagegen die Zahl 28 die Regel, wie ich bei zwei Individuen

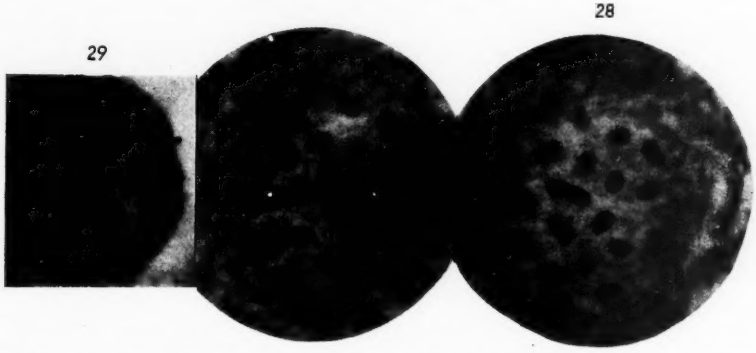


Fig. 25. *Argynnis adippe* L. Spermatozytenplatte I mit 29 Chromosomen, Oozytenplatte in zwei Aufnahmen mit 28 Chromosomen.

der Hauptform und einem Weibchen der ab. *cleodoxa* O. feststellen konnte. In 35 Oozytenplatten I habe ich 28 Chromosomen gezählt.

Wie Fig. 25 zeigt, kommt auch hier ein grosses Chromosom in der Oozyte vor. Es liegt in der linken Platte links unten und wird nach links schmäler. Zwi-

schen diesem schmäleren Ende und dem dickeren Hauptteil kann man oft eine Furche entdecken, die deutlich verrät, dass das Chromosom aus einem grossen und einem kleinen zusammengesetzt ist.

Arg. paphia. — In 70 Spermatozyten I und II eines Männchens habe ich exakt 29 Chromosomen gezählt; nur in einer Platte war deren Anzahl 30. Die beiden in Fig. 26 photographierten Platten I zeigen deutlich, dass zwei Chromosomen durch ihre bedeutende Grösse auffallen.

Die zwei von mir untersuchten Weibchen hatten, wie die zwei vorher beschriebenen Arten, in ihren Oozyten I 28 Chromosomen, worunter aber nicht ein, sondern

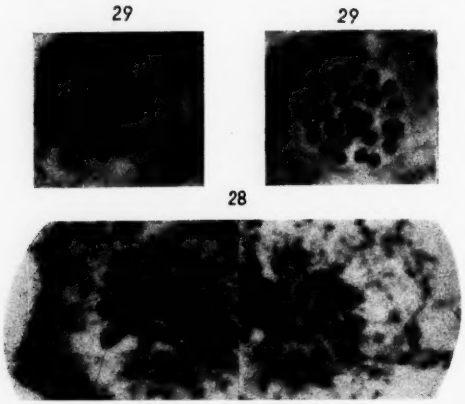


Fig. 26. *Argynnis paphia* L. Spermatozytenplatten I mit 29 Chromosomen, Oozytenplatte mit 28 Chromosomen in zwei Aufnahmen.

zwei lange Chromosomen, in Fig. 26 links 8 Uhr, rechts 2 Uhr. In ganz vereinzelten Platten konnten 29 Chromosomen gezählt werden, und in diesen Platten kam nur *ein* grosses Chromosom vor.

SATYRINÆ.

Diese Familie scheint, nach den 14 von mir untersuchten Arten zu urteilen, in bezug auf die Chromosomenzahl recht einheitlich zu sein. Bei 12 Arten finden wir nämlich die Zahlen 28 und 29. Auffallenderweise vertreten von den beiden übrigen Arten die eine die Mindestzahl bei den Schmetterlingen überhaupt, die andere die Höchstzahl unter den Rhopaloceren. *Erebia medusa* v. *polaris* hat nämlich nur 11 Chromosomen, *Oeneis jutta* wiederum 32.

Erebia medusa v. *polaris.* — Mag. NORDMAN verdanke ich zwei Ovarien dieser eigentümlichen, bloss in Lappland, Utsjoki, fliegenden Varietät der nur in Mitteleuropa vorkommenden Hauptart. Die Ovarien enthielten leider eine verhältnismässig geringe Anzahl Eier. Es war mir jedoch möglich, an 4 unzerschnittenen Oozytenplatten und dazu noch an drei auf zwei Schnitte verteilten Kernen die Chro-

mosomenzahl exakt festzustellen. Sie beträgt nur *11*, und als Lepidopterenchromosomen müssen diese Chromosomen als *ungeheuer gross* bezeichnet werden. Infolge ihrer Grösse und Länge liegen sie offenbar nur selten in einer Ebene. Fig. 27 zeigt uns zwei Reifemitosen, die in drei, resp. vier Aufnahmen mit verschiedener Einstellung photographiert sind, und ausserdem eine Aufnahme einiger Chromosomen einer dritten Spindel. Die Bilder geben eine Vorstellung von der Grösse und Form der Chromosomen.

Es wäre von grossem Interesse zu erfahren, ob die in Mitteleuropa fliegende

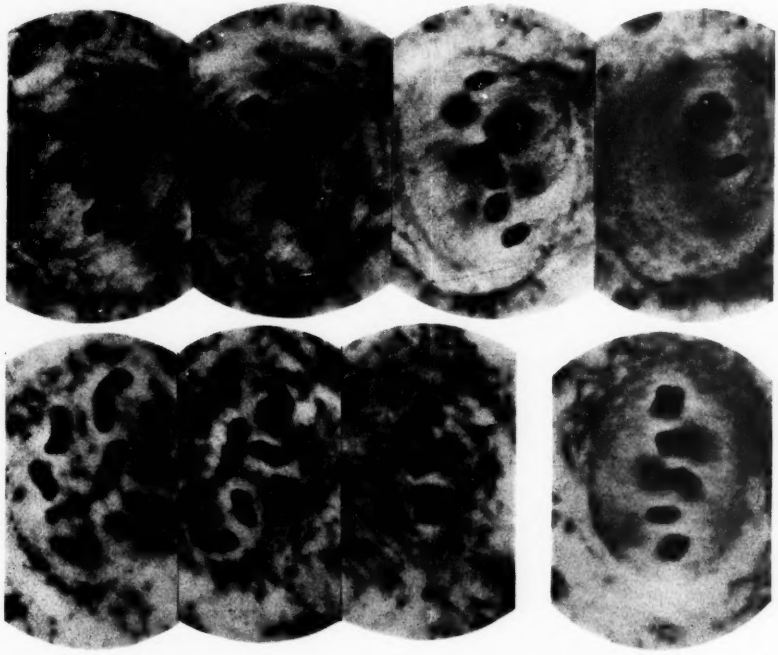


Fig. 27. *Erebia medusa* F. v. *polaris* STAUD. Drei Oozytenmitosen I. In der oberen Reihe vier Aufnahmen, die alle 11 Chromosomen zur Schau bringen. In der unteren Reihe eine jüngere Metaphase in drei Aufnahmen, daneben eine Reifemitose in Profil.

Hauptform auch dieselbe Chromosomengarnitur aufweist, oder ob die als Relikt betrachtete hochnordische Varietät durch eine Mutation diese geringe Zahl von Chromosomen erhalten hat.

E. ligea. — Von zahlreichen frischen Männchen habe ich die Testes fixiert, sie enthielten aber lauter Spermien und vereinzelte apyrene Teilungen, in denen die Chromosomenzahl nicht exakt festgestellt werden kann.

In einigen Oozytenplatten I von einem in Pojo und zwei in Pernå gefangenen Faltern habe ich dagegen sicher *29* Chromosomen zählen können.

E. lappona. — Von dieser nur in Lappland und auf den norwegischen Fjelden fliegenden Art stand mir ein von Mag. NORDMAN fixiertes Ovarium zur Verfügung. Es stammt von einem in Utsjoki gefangenen Weibchen.

Das Ovar enthielt vier ganz klare Platten mit 28 Chromosomen und ausserdem drei zerschnittene Kerne, die sicher auch 28 Chromosomen besitzen. Fig. 28

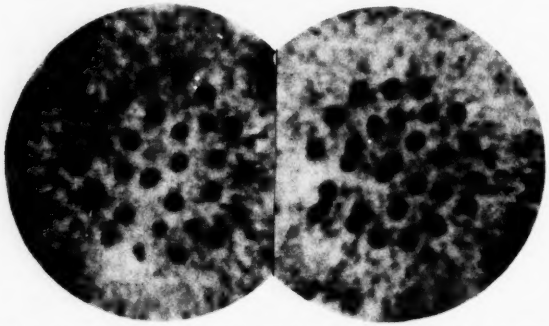


Fig. 28. *Erebia lappona* ESP. Zwei Oozytenplatten I mit 28 Chromosomen. In beiden liegt das grosse Chromosom ausserhalb der eigentlichen Platte und in einer etwas anderen Ebene als die übrigen Chromosomen, weshalb es kleiner erscheint.

zeigt uns zwei Platten. Wie aus diesen ersichtlich ist, kommt in den Platten ein grösseres Chromosom vor, das meistens ausserhalb der eigentlichen Platte liegt. In der Platte links finden wir es bei 10 Uhr, in der Platte rechts bei 8 Uhr. In beiden Platten erscheint es viel zu klein, weil es in einer anderen Ebene als die übrigen Chromosomen liegt.

E. disa. — Durch die Güte von Mag. SUOMALAINEN habe ich ein von ihm fixier-

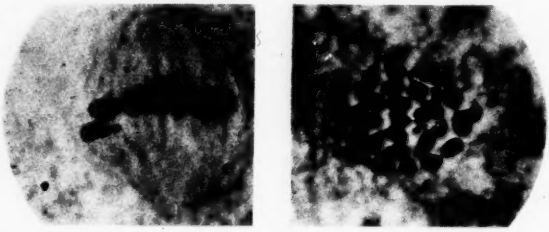


Fig. 29. *Oeneis jutta* HB. Oozyten I. Platte mit 32 Chromosomen und Satelliten. Links Spindel in Profil, Satellit sehr deutlich.

tes Ovarium dieser hochnordischen Art erhalten. Das Weibchen war in Kuusamo erbeutet.

Leider enthielt die Schnittserie des Ovars keine einzige ganze Platte, doch konnte an drei zerschnittenen Platten die Zahl der Chromosomen ganz sicher als 29 festgestellt werden.

Oeneis jutta. — Vier Testes von jungen Imagines enthielten keine Reifeteilungen.

Nur ein Weibchen habe ich erbeuten können; es gehört zu den interessantesten der von mir untersuchten Arten. Zunächst besitzt es die grösste Chromosomenzahl unter den Rhopaloceren, nämlich *32*, wie *Papilio machaon* in Finnland. Unter diesen Chromosomen sind zwei bedeutend kleiner als die übrigen, die unter einander einigermassen gleich gross sind. Sodann besitzen viele von den grösseren Chromosomen *Satelliten*. In der in Fig. 29 wiedergegebenen Oozytenplatte I kann man

Fig. 30. *Satyrus semele* L. Oozytenplatte I in drei Aufnahmen und Spermatozytenplatte I, beide mit 29 Chromosomen.

nur 31 Chromosomen deutlich unterscheiden, weil eines von den kleinen nicht klar zum Vorschein kommt. Die Satelliten treten auch nicht deutlich hervor, weil sie eine ganz besonders genaue Einstellung fordern. Das Profilbild ist genau auf den Satelliten eingestellt, weshalb er auch scharf gezeichnet ist. Das stärkere oder schwächere Hervortreten der Satelliten ist selbstverständlich in erster Linie von der Stärke der Differenzierung abhängig. Es ist deshalb eine schwere Aufgabe ihre Anzahl exakt festzustellen. Ich möchte sie auf 6—8 schätzen. Sechs habe ich nämlich ganz sicher zählen können. Die Satelliten gehören immer zu den grossen Chromosomen; die beiden kleinen haben niemals Satelliten.

Satyrus semele. — In einem Testis eines jungen Imagos habe ich in 16 Spermatozytenplatten I *29* Chromosomen gezählt und nur in einer 28. In 8 Platten II war die Zahl auch 29.

In 13 Oozytenplatten I wurde gleichfalls die Zahl *29* festgestellt. Wie Fig. 30 zeigt, sind sich die Chromosomen der Grösse und Form nach sehr ähnlich.

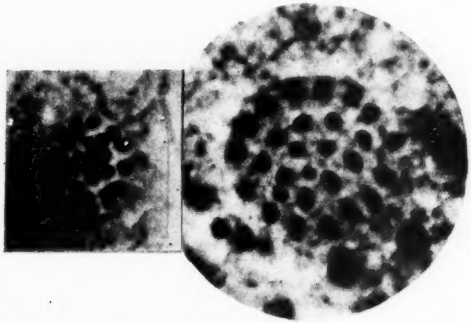


Fig. 31. *Pararge ægeria* L. v. *ægerides* STGR. Spermatozyte I und Oozyte I, beide mit 28 Chromosomen.

Pararge ægeria v. *ægerides*. — Ein von Mag. SUOMALAINEN in der Umgebung von Helsingfors gefangenes Paar wurde mir zur Verfügung gestellt.

Das Männchen enthielt noch fünf Spermatozytenplatten I, in denen *28* Chromosomen einwandfrei gezählt werden konnten. Vgl. Fig. 31.

Im Ovar konnte in drei Platten dieselbe Zahl *28* festgestellt werden, wie Fig. 31 zeigt.

P. hiera. — Nur in einem von vielen untersuchten Testes habe ich in einigen Spermatozyten II die Chromosomenzahl *29* feststellen können.

Bei zwei Weibchen habe ich in den Oozytenplatten I dieselbe Zahl *29* gefunden.

P. mæra. — In drei Testes wurde in insgesamt 28 Spermatozyten I und II exakt *28* Chromosomen gezählt. Unter diesen fällt eines durch erheblichere Grösse auf. Vgl. Fig. 32.

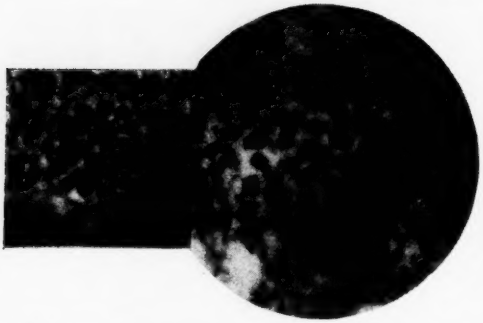


Fig. 32. *Pararge mæra* L. Spermatozyte I und Oozyte I mit 28 Chromosomen.

In einem Ovar konnte in drei Oozytenplatten I die Chromosomenzahl als genau *28* festgestellt werden. Auch hier kann man ein grösseres Chromosom von den übrigen unterscheiden, wie die klare Platte der Fig. 32 darlegt.

Aphantopus hyperantus. — Mehrere Schnittserien von Imagotestes zeigten lauter apyrene Reifeteilungen.

In zahlreichen Oozytenplatten I von Weibchen aus verschiedener Gegenden konnten dagegen *29* Chromosomen sicher gezählt werden.

Epinephele jurtina. — Drei Testes enthielten zusammen 17 Spermatozytenplatten I, die alle *29* Chromosomen besassen.

Die Oozytenplatten I sind ebenfalls durch die Zahl *29* charakterisiert. Obwohl

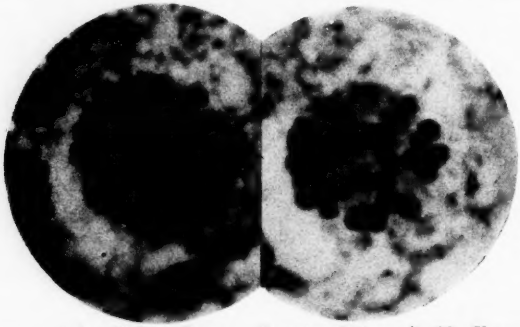


Fig. 33. *Coenonympha tiphon* ROTT. Oozytenplatte mit 29 Chromosomen, ein wenig agglutiniert, in zwei Aufnahmen.

mir leider nur wenige wirklich klare Platten zur Verfügung standen, scheint mir die Zahl 29 doch ganz sicher zu sein.

Coenonympha iphis. — Eine beträchtliche Anzahl genau untersuchter Testes aus neuausgeschlüpften Männchen enthielt keine Reifeteilungen.

In einigen Oozytenplatten von drei Weibchen ist es mir dagegen gelungen die Chromosomenzahl genau festzustellen; sie beträgt *29*.

C. tiphon. — Auch bei dieser Art enthalten die Testes der Imagines keine Reifeteilungen.

Die Oozytenplatten sind denjenigen der vorigen Art ganz gleich und haben auch *29* Chromosomen (Fig. 33).

C. pamphilus. — Die Spermatogenese scheint bei den meisten Imagines so weit vorgeschritten zu sein, dass keine Reifeteilungen mehr vorkommen. In einem einzigen von vielen Testes gelang es mir jedoch, eine Zyste mit Spermatozyten in der ersten Reifeteilung zu finden; in zwei von diesen konnte die Zahl *29* genau festgestellt werden.

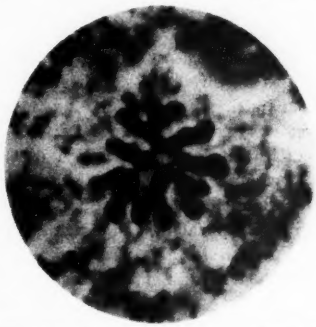


Fig. 34. *Coenonympha pamphilus* L. Oozytenplatte mit 29 stark agglutinierten Chromosomen.

Die Oogenese habe ich an Exemplaren aus der Gegend von Borgå (Mag. SUOMALAINEN) und aus dem Kirchspiel Snappertuna untersucht. Bei einem Weibchen aus Borgå habe ich in zwei Platten sicher *28* Chromosomen zählen können und in drei weiteren nicht ganz klar 27—28. Das Snappertuna-Weibchen enthielt dagegen eine vorbildlich schöne Platte mit *29* Chromosomen. Es scheint demnach, als ob hier sowohl ein Typus mit 28 wie auch ein solcher mit 29 Chromosomen vorkäme. Das Männchen mit 29 Chromosomen stammte gleichfalls aus Snappertuna. Eine endgültige Bestätigung dieser Vermutung kann selbstverständlich erst nach Untersuchung eines grösseren Materials erlangt werden.

Fig. 34 zeigt eine wenig schöne Oozytenplatte mit 29 stark agglutinierten Chromosomen.

LYCÆNIDÆ.

Auch die Lycæniden scheinen, sofern man sich auf Grund der 15 von mir untersuchten Arten ein allgemeines Urteil erlauben darf, eine in bezug auf die Chromosomenzahl sehr einheitliche Familie zu bilden. 13 Arten haben nämlich 23 oder 24 Chromosomen, und eine höhere Zahl kommt nur bei der Art *Cyaniris argiolus* vor, die 25 Chromosomen besitzt. Auffallenderweise kommt auch hier, wie in den drei vorher behandelten Familien, eine Art vor, die eine weit geringere Zahl von sehr grossen Chromosomen aufweist. *Zephyrus betulæ* hat nämlich nur etwa 16 lange und kräftige Chromosomen. Aber nicht nur die Chromosomenzahl ist bei der grossen Mehrzahl der Arten dieselbe, auch der Karyotypus selbst zeigt eine auffallend grosse Ähnlichkeit. In den Oozyten ist der Kern in der Regel infolge des reichlich vorhandenen Karyoplasmas und der späten Auflösung der Kernmembran leicht zu finden. Die Chromosomen liegen auch öfters recht weit voneinander entfernt, obgleich Kettenbildung in einem früheren Stadium durchaus nicht selten zu sein braucht.

Callophrys rubi. — Die Testes der Imagines enthalten lauter apyrene Spermatozyten und reife Spermien.

Das einzige untersuchte Weibchen enthielt einige Oozyten mit sehr schönen Platten, in denen die Zahl *23* genau festgestellt werden konnte.

Zephyrus betulæ. — Durch Vermittlung von Mag. SUOMALAINEN wurde mir ein lebendiges Weibchen dieser bei uns seltenen Art aus Karis-Lojo zugesandt. Leider erwies es sich, dass die Fixierung der Eier grosse Schwierigkeiten bereitet. Die überwinternden Eier haben nämlich eine sehr dicke Schale, die ausserdem von grossen Hohlräumen durchsetzt ist. Unter solchen Verhältnissen ist es klar, dass das Eindringen der Fixierungsflüssigkeit nur sehr langsam erfolgen kann. Trotzdem das gut und schnell durchdringende Gemisch von CARNOY zur Fixierung gebraucht wurde, erwiesen sich die Eier schlecht fixiert. Die Kernmembran scheint ausserdem schlecht permeabel zu sein. Da nun überdies die harte und dicke Schale beim Schneiden sehr lästig ist, und die Eier demzufolge zerrissen werden, wurden in den Präparaten verhältnismässig wenig gute Kerne gefunden und von diesen die allermeisten in Profilansicht.

Es war mir infolgedessen nicht möglich, die Chromosomenzahl exakt festzu-

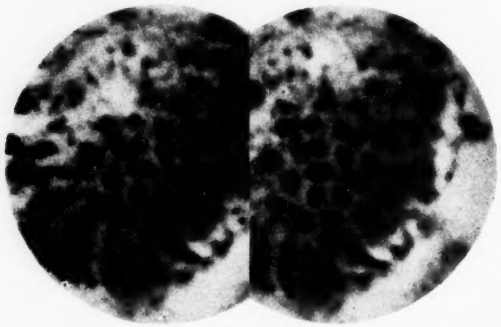


Fig. 35. *Chrysophanus hippothoë* L. Oozytenplatte I mit 24 Chromosomen in zwei Aufnahmen.

stellen. So viel ist indessen klar, dass die Chromosomen *sehr gross* und an der Zahl *gering* sind. Ich möchte die Anzahl auf etwa *16* schätzen; weniger als 14 sind es sicher nicht und mehr als 18 kaum.

Chrysophanus virgaureæ. — Vier Testes wurden geschnitten; in 15 Spermatozyten I und in zwei Spermatozyten II wurden exakt *24* Chromosomen gezählt; ausserdem konnten die Zahlen 25 und 26 in zwei Kernen festgestellt werden. Die kleinen Chromosomen dieser Kerne deuten auf Fragmentierung hin.

In Ovarien von zwei Imagines habe ich in fünf Platten genau die Chromosomenzahl *24* nachweisen können. Die Chromosomen sind, verglichen miteinander, ziemlich gleich gross; nur eines von ihnen bildet eine Ausnahme, indem es auffallend klein ist.

Chr. hippothoë. — Es wurde nur ein Testis untersucht, das jedoch keine Reifeteilungen enthielt.

Die Ovarien von drei Imagines wurden geschnitten; sie hatten zusammen 23 Platten, in denen man die Chromosomenzahl *24* ganz genau feststellen konnte. Alle sind von annähernd gleicher Grösse; keines ist auffallend klein wie bei *virgaureæ*. Fig. 35 gibt eine Oozytenplatte I wieder.

Chr. phlæas. — Der Testis einer jungen Imago enthielt 11 Platten I und eine Platte II mit *24* Chromosomen.

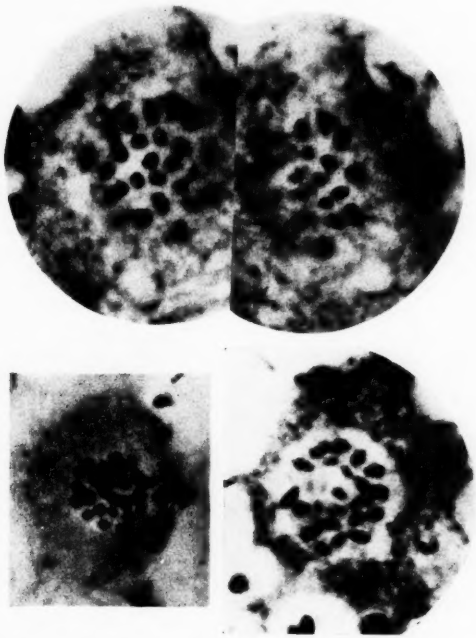


Fig. 36. *Chrysophanus phlæas* L. Oben eine Oozytenplatte I in zwei Aufnahmen; unten links eine Spermatozytenplatte I und eine Oozytenplatte I, alle mit 24 Chromosomen, von denen drei in der unteren Oozytenplatte in der Mitte nur unbedeutend hervortreten.

Nur ein Ovarium wurde untersucht; es gelang mir in diesem 18 Platten I mit *24* Chromosomen zu finden.

Fig. 36 gibt eine Spermatozytenplatte I und zwei Oozytenplatten I wieder.

Lycæna argus. — In drei Testes wurde zusammen in 16 Platten I und in 5 Platten II die Chromosomenzahl *23* festgestellt. Vgl. Fig. 37.

Fig. 37. *Lycæna argus* L. Spermatozytenplatte I mit 23 Chromosomen.

In Ovarien von zwei Imagines wurden 8 Oozytenplatten I gefunden, die gleichfalls *23* Chromosomen erkennen liessen.

L. argyrognomon. — In zwei Testes konnte an 11 Platten I und II die Chromosomenzahl *24* konstatiert werden (Fig. 38).

Ovarien von zwei Weibchen liessen an zusammen 7 Oozytenplatten I dieselbe Zahl *24* erkennen. In Fig. 38 sind zwei solche Platten wiedergegeben. Die Platte

links ist älter und zeigt klar und deutlich 24 Chromosomen (das lange horizontal liegende besteht aus zwei Chromosomen, die in der Photographie fast miteinander vereinigt sind). Die Platte rechts ist jünger. Die endgültige Verkürzung der Chromosomen hat noch nicht stattgefunden, weshalb die Chromosomen länger und weniger scharf umrandet sind. Drei Chromosomen in der Sektion 12—2 Uhr treten nur wie Schattenflecke auf, weil sie in einer niedrigeren Ebene liegen.

Keines von den Chromosomen ist auffallend gross oder klein.

Es ist bemerkenswert, dass die beiden Arten *argus* und *argyrognomon*, deren Weibchen einander so ähnlich sind, dass sie bloss je nach dem Vorhandensein oder Fehlen eines Stachels an der Vordertibie voneinander unterschieden werden können, eine verschiedene Chromosomenzahl besitzen.

L. optilete. — Trotzdem mehr als ein Dutzend Hoden von ganz jungen Imagines geschnitten wurden, gelang es mir nur einen einzigen Testis zu finden, der ganz

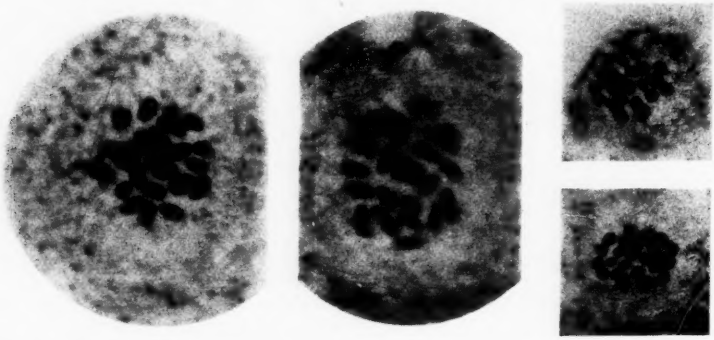


Fig. 38. *Lycæna argyrognomon* BERGSTR. Zwei Oozytenplatten I mit 24 Chromosomen. Die rechts stehende jünger mit längeren Chromosomen, von denen die drei oben rechts (12—2 Uhr) nur durch Schattenflecke angedeutet sind. Zwei Spermatozytenplatten I mit 24 Chromosomen.

vereinzelte Reifeteilungen aufwies. Diese enthielten alle 24 Chromosomen. Die Reifeteilungen dieser Art finden offenbar schon in der Puppe oder Raupe statt.

Das einzige von mir untersuchte Ovarium enthielt einige sehr klare Platten mit 24 Chromosomen. In Fig. 39 sind zwei solche Platten gezeichnet. Die obere Platte befindet sich noch im Übergang von der Prophase in die Metaphase, weshalb die Chromosomen länger sind und eine rauhe Oberfläche haben.

L. astrarche. — Zu meiner Verfügung standen nur ein Männchen aus Tvärminne, gefangen von Mag. NORDMAN, und ein Weibchen aus Kuusamo, Nordfinnland, wo das Ovarium von Mag. SUOMALAINEN fixiert wurde.

Der Hoden enthielt 15 Platten von Spermatozyten I und II, in denen genau 23 Chromosomen gezählt werden konnten. Unter diesen fällt ein Chromosom durch seine Grösse auf. In Fig. 40 tritt es in der Spermatozyte I besonders deutlich hervor, wogegen es in der Spermatozyte II niedriger liegt und deshalb nur als ein Schattenfleck links unten zum Vorschein kommt. Dieses grosse Chromosom teilt sich in der ersten Reifeteilung weit später als die übrigen Chromosomen und hinkt

in der späteren Anaphase nach. Wie Fig. 40 deutlich zeigt, ist es jetzt schon längsgespalten.

Im Ovarium gab es zahlreiche Eier; nur in fünf konnte jedoch die Chromosomenzahl ganz einwandfrei festgestellt werden. Sie beträgt 24, wie Fig. 40 beweist. Unter den Chromosomen kommt kein auffallend grosses vor, wie in den Spermatozyten.

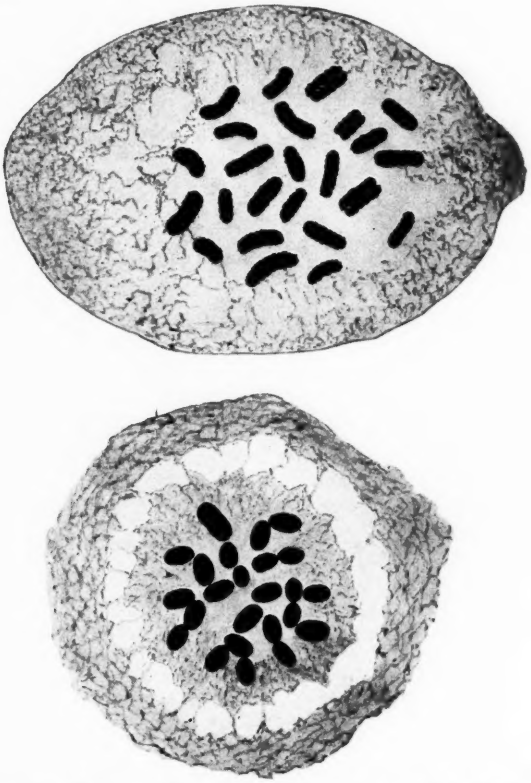


Fig. 39. *Lycæna optilete* KNOCH. Oben, eine ganz junge Oozytenplatte I mit 24 langen noch rauhen Chromosomen; Kernmembran noch nicht aufgelöst. Unten, alte Platte mit 24 ovalen glatten Chromosomen. Beide gezeichnet.

Nach diesen beiden Individuen zu beurteilen, deren eines aus dem südlichsten Finnland, das andere aus dem Norden stammte, liegen die Verhältnisse bei dieser Art, verglichen mit denen bei den *Argynnis*-Arten *niobe*, *adippe* und *paphia*, umgekehrt. Während bei den *Argynnis*-Arten die Weibchen ein Chromosom weniger haben als die Männchen, besitzt das Weibchen von *astrarche* ein Chromosom mehr. In beiden Fällen erscheint es als wahrscheinlich, dass der Unterschied durch Fusion

zweier Chromosomen entstanden ist, bei den *Argynnis*-Arten im weiblichen, bei *astrarche* im männlichen Geschlecht. Da das Material von *astrarche* jedoch aus geographisch weit getrennten Gegenden stammt, ist es nicht ausgeschlossen, dass der Unterschied kein geschlechtlicher, sondern ein geographischer Rassenunterschied sein könnte. Hier müssten ergänzende Untersuchungen ausgeführt werden.

L. eumedon. — Von dieser Art wurde ein Weibchen von Mag. SUOMALAINEN in der Nähe von Mariehamn, Åland, erbeutet und fixiert.

Das Ovarium enthielt zahlreiche Eier; in sieben Platten konnten die Chromosomen genau gezählt werden. Es sind *24* an der Zahl.

L. icarus. — Das Material stammt zum Teil aus Pojo, zum Teil aus Pernå. Irgend einen Unterschied zwischen den Individuen aus den beiden Kirchspielen habe ich nicht entdecken können.

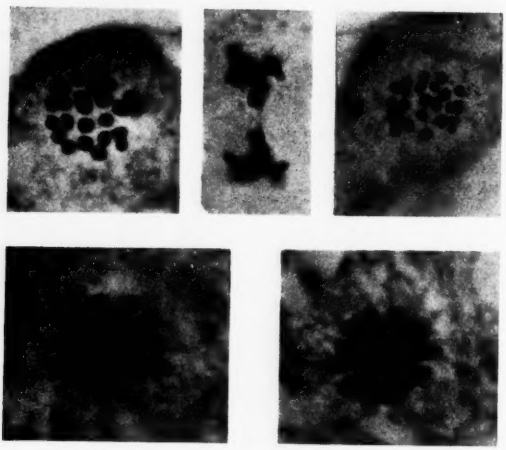


Fig. 40. *Lycæna astrarche* BERGSTR. Oben: Spermatozytenplatten I und II mit 23 Chromosomen, darunter ein grosses; in der Mitte eine Anaphase I mit nachhinkendem, gespaltenem, grossem Chromosom. Unten: zwei Oozytenplatten I mit 24 Chromosomen, unter denen kein grosses.

Nur ein einziger Testis wurde untersucht; in sechs Platten konnte die Zahl *23* genau festgestellt werden; ausserdem kamen auch vereinzelte Spermatogonienplatten vor, in denen es möglich war, mit ziemlich grosser Sicherheit *46* Chromosomen zu zählen. In Fig. 41 sind drei Spermatozytenplatten I und eine Spermatogonienplatte nach Zeichnungen wiedergegeben. In den erstgenannten fällt ein Chromosom durch seine bedeutende Grösse auf, in der letztgenannten entdeckt man zwei längere Chromosomen.

Vier Ovarien wurden geschnitten. An dem in Pojo erbeuteten Weibchen kann in 12 Oozytenplatten die Chromosomenzahl *23* festgestellt werden, wobei das lange Chromosom stets mit einem ganz kleinen verbunden ist, wie die beiden gezeichneten Oozyten der Fig. 41 deutlich zeigen. Eines von den in Pernå gefangenen Weibchen hat 18 ganze und 4 zerschnittene Platten mit 23 Chromosomen, das zweite

hat 3 Platten mit 23 und 4 Platten mit 22 Chromosomen und das dritte schliesslich 8 ganze und 5 zerschnittene Platten, sämtliche mit 22 Chromosomen. Hierbei ist

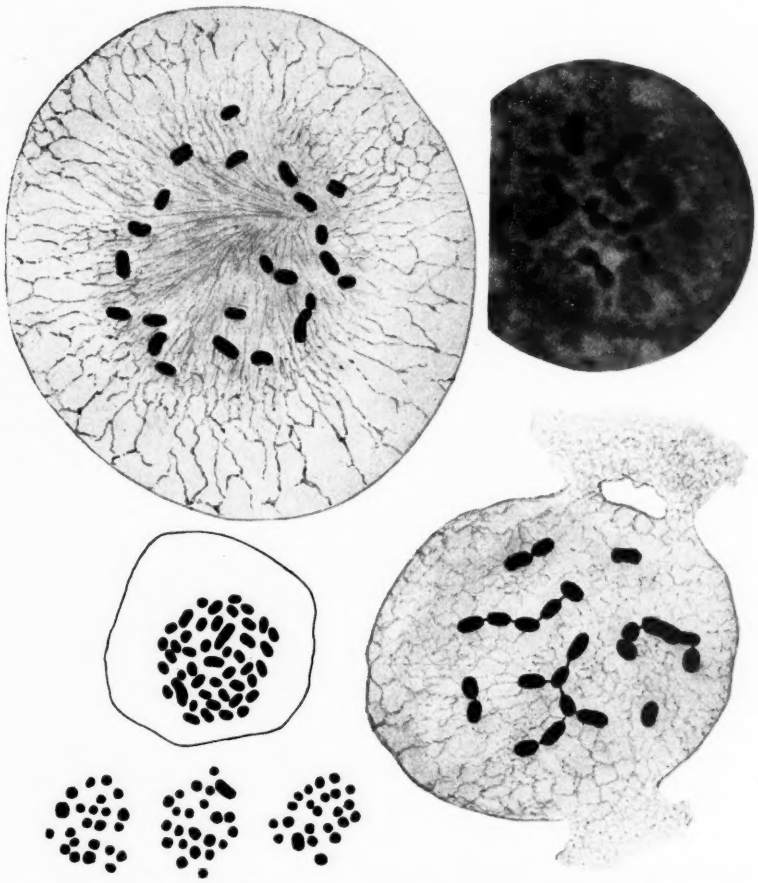


Fig. 41. *Lycæna icarus* ROTT. Links unten: Spermatogoniumplatte mit 46 Chromosomen, unter diesen 2 lange, drei Spermatozytenplatten mit 23 Chromosomen, ein langes. Oben links: Prometaphase der I. Oozytenteilung mit 23 Chromosomen, das lange in Fusion mit einem kleinen (bei 4—5 Uhr). Oben rechts: Oozytenplatte I, das fusionierte Paar bei 11 Uhr. Unten rechts: Oozytenplatte I, das fusionierte Paar bei 3 Uhr. Mit Ausnahme der Photographie oben rechts alle Abbildungen gezeichnet.

zu bemerken, dass alle Platten mit 23 Chromosomen ein langes Chromosom aufweisen, das mit einem kurzen verbunden ist, wie dies mit dem Pojo-Weibchen der Fall war. Dagegen haben die Platten mit 22 Chromosomen ein sehr langes Chro-

mosom, das der Länge nach dem langen und dem kurzen zusammen entspricht. Alles spricht also dafür, dass dieses sehr lange Chromosom durch eine Fusion des langen und des kurzen Chromosoms entstanden ist.

In den jungen wachsenden Oozyten des Pojo-Weibchens kommt ein eigenartiges Gebilde vor, das im Gegensatz zu den zu dieser Zeit rauhen Chromosomen

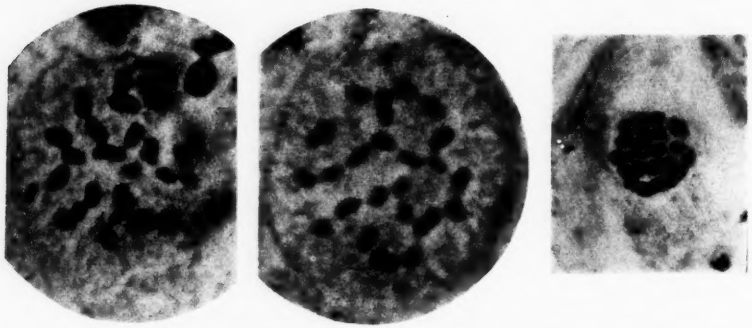


Fig. 42. *Lycæna amandus* SCHN. Zwei Oozytenplatten I und eine Spermatozytenplatte I mit 23 Chromosomen.

glatt und stark ausgedehnt ist. Da es in vielen Oozyten in ganz ähnlicher Weise auftrat, fasste ich es seinerzeit als ein Idiochromosom auf, das sich durch Heteropyknose von den Autosomen unterscheidet (FEDERLEY, 1925). In den drei aus Pernå stammenden Weibchen habe ich ein entsprechendes Gebilde nicht entdecken können, und ich muss die Deutung dieses rätselhaften Gebildes bis auf weiteres offen lassen.

L. amandus. — Zwei Männchen und ein Weibchen wurden untersucht.

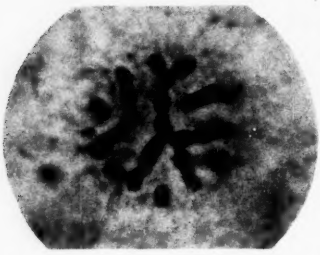


Fig. 43. *Lycæna arion* L. Oozytenplatte I mit 23 Chromosomen.

In den beiden Testes konnten in 26 Spermatozytenplatten I *23* Chromosomen gezählt werden. Fig. 42 gibt eine solche nicht besonders schöne Platte wieder.

Das Weibchen besass 9 Oozyten I, in denen es möglich war die Zahl *23* genau festzustellen. Zwei Oozytenplatten finden wir in Fig. 42. Eine Tendenz zur Fusion von zwei Chromosomen ist nicht vorhanden.

L. semiargus. — Die untersuchten Testes enthielten lauter apyrene Spermien.

Zwei Ovarien wurden untersucht. In 13 Platten wurde die Chromosomenzahl *24* festgestellt.

L. arion. — Der einzige untersuchte Testis enthielt keine Reifeteilungen, dagegen hübsche eupyrene Diakinesen, in denen jedoch die Chromosomenzahl schwer genau festgestellt werden kann. Auch recht gute Spermatogonienteilungen kamen vor, jedoch nicht so gut fixierte, dass eine genaue Feststellung der diploiden Chromosomenzahl möglich gewesen wäre.

Ein reifes Ovarium enthielt dagegen sehr zahlreiche Oozytenplatten I. In 18 derselben konnten genau 23 Chromosomen gezählt werden, und unter diesen fielen regelmässig zwei besonders lange auf. In Fig. 43 sind sie deutlich zu sehen. Ihre Lage ist nicht bestimmt; zuweilen treten sie in der Chromosomenkette hintereinander auf, meistens aber sind sie weit voneinander getrennt wie in der photographierten Platte, wo sie bei 2 und 7 Uhr zu finden sind.

Cyaniris argiolus. — Alle gefangenen Männchen waren viel zu alt, um Reifeteilungen zu besitzen.

Zwei Weibchen dagegen enthielten einzelne Oozytenplatten I, in denen 25 Chromosomen deutlich gezählt werden konnten. Unter diesen ist keines besonders gross, aber zwei sind ein wenig grösser als die übrigen.

HESPERIDÆ.

Von den vier Gattungen mit zusammen neun Arten habe ich leider nur vier Vertreter erhalten können, aber unter diesen eine Art, die in den Ovarien beide Reifeteilungen aufweist.

Thymelicus lineola. — Die Reifeteilungen finden im Testis schon auf dem Puppenstadium statt, denn von vier geschnittenen Testes enthielt nur einer wenige Reifeteilungen. In drei Spermatozytenplatten I konnten ganz eindeutig 29 Chromosomen beobachtet werden.

Nur ein Ovarium wurde geschnitten, und in diesem gab es nur eine Platte, in der genau 29 Chromosomen gezählt werden konnten. Vgl. Fig. 44. In einigen auf zwei Schnitte verteilten Platten wurde dieselbe Zahl beobachtet. Die Platten sind auffallend klein. Man vergleiche Fig. 44 mit Fig. 47.

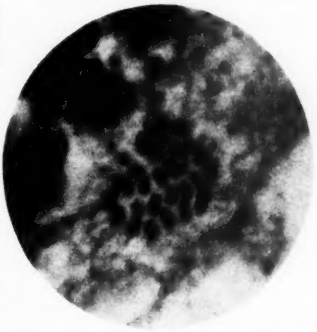


Fig. 44. *Thymelicus lineola* L. Oozytenplatte I mit 29 Chromosomen; der kleine Fleck ausserhalb der Peripherie bei 10 Uhr ist kein Chromosom.

Augiades sylvanus. — Es wurden 8 Testes aus jungen Imagines geschnitten. Nur zwei von diesen enthielten Reifeteilungen und sogar in erheblicher Zahl. Es wurden 10 hübsche Platten in der ersten und 24 in der zweiten Reifeteilung gefunden, in denen sich die Chromosomenzahl einwandfrei als 29 erwies. In Fig. 45 sind zwei photographiert; in der Platte I links ist ein Chromosom (9 Uhr) nur durch einen schwachen Schatten angedeutet.

Die Oogenese dieser Art ist von besonderem Interesse, denn die erste Reifeteilung findet hier häufig schon im Ovarium in dem unbefruchteten Ei statt. In den ältesten Eiern kann man nämlich nicht nur Anaphasen der ersten Reifeteilung finden, sondern auch Metaphasen der zweiten. Ich habe aus diesem Grunde sieben Ovarien geschnitten, und in drei von diesen war die Oogenese bis zur zweiten Reifeteilung vorgeschritten. In allen sieben Ovarien wurde in der ersten Reifeteilung die Zahl 29 festgestellt. Es waren zusammen 13 Platten. Da das Material aus Pernå und aus Snappertuna stammt, dürfte die Zahl 29 wohl als einzige Zahl angesehen werden können, um so mehr, als ausserdem zahlreiche zerschnittene Platten dieselbe

Zahl aufwiesen. Die genaue Feststellung der Zahl ist nämlich für die Beurteilung der zweiten Reifeteilung und eines eventuellen Vorkommens von Geschlechtschromosomen von grosser Bedeutung.

Es ist mir gelungen, nur drei Eier zu finden, in denen man die Chromosomen in den beiden Platten der zweiten Reifeteilung zählen kann, und leider liegen die

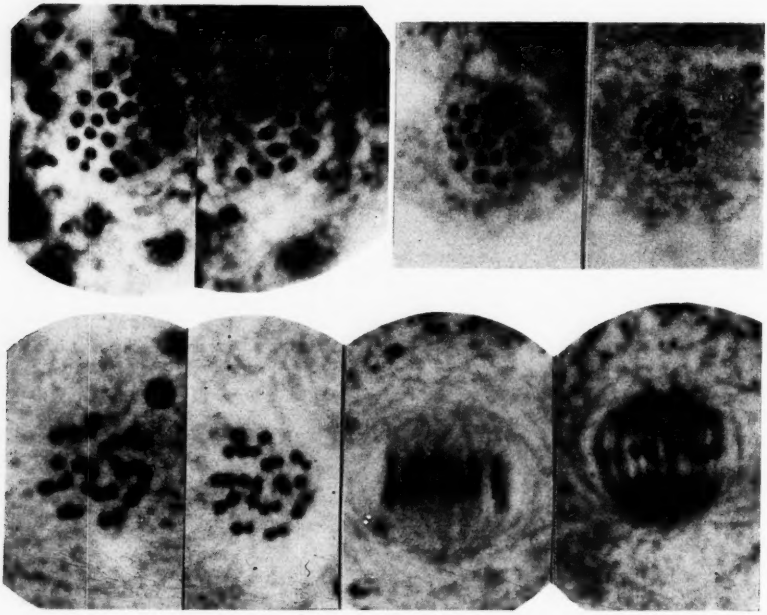


Fig. 45. *Augiades sylvanus* Esp. Oben rechts: Spermatozytenplatten I und II mit 29 Chromosomen; in der Platte links ein Chromosom bei 10—11 Uhr an der Peripherie nur blass angedeutet. Oben links: Oozytenplatte I mit 29 Chromosomen in zwei Aufnahmen. Unten links: Zwei Oozytenplatten II aus demselben Ei; in der unteren (links) kommt ein Chromosom, das in der oberen (rechts) bei 11 Uhr deutlich ist, nicht zum Vorschein, weil es in einem anderen Schnitt liegt; in der oberen (rechts) sind zwei Chromosomen in der Photographie bei 3—4 Uhr an der Peripherie so gut wie unsichtbar; in der unteren ist das eine von diesen auch undeutlich. Untere Platte mit 28, obere mit 29 Chromosomen, in der unteren fehlt das Chromosom bei 9 Uhr an der Peripherie, wogegen es klar in der oberen hervortritt. Unten rechts: Anaphase der Oozytenteilung I, in der rechten eine deutliche Eliminationsplatte.

Verhältnisse auch in diesen nicht vollständig klar. Ich werde die drei Eier jedes für sich beschreiben.

1. Hier kann man die beiden Chromosomenplatten und die Eliminationsplatte deutlich sehen. Die Chromosomenplatten sind in Fig. 45 photographiert. Das Mikrotommesser hat die obere Platte (Polplatte) nebst der Eliminationsplatte von der unteren oder der Oozytenplatte II getrennt. Von dieser ist jedoch ein

Chromosom ganz an der Peripherie (11 Uhr) entfernt worden und ist auf dem oberen Schnitt wiederzufinden. Wie den Photographien zu entnehmen ist, können die in den Platten einander entsprechenden Chromosomen mit grosser Leichtigkeit identifiziert werden. Eine Verschiebung der getrennten Chromosomen hat noch nicht stattgefunden, und die Präparate sind demzufolge ungewöhnlich klar. In der Photographie der oberen Platte sind indessen zwei Chromosomen an der Peripherie rechts (3 Uhr) infolge ihrer niedrigeren Lage nicht zu sehen; im Präparat sind sie dagegen vollständig klar. Zählen wir die Chromosomen der beiden Platten, so erhalten wir in der oberen 29, in der unteren dagegen nur 28 (in der Photographie nur 27, weil ein Chromosom in dem oberen Schnitt liegt). Es ist auch leicht anzugeben, welches Chromosom in der unteren Platte fehlt; es ist das äusserste an der Peripherie gelegene (9 Uhr). In der Eliminationsplatte kann man dieses Chromosom noch sehen und gleich unterhalb dieser, in derselben Ebene wie das aus der unteren Platte entfernte Chromosom (11 Uhr), kommt ein ganz kleiner heller Fleck zum Vorschein. Es könnte sich also um ein *XY*-Paar handeln, sofern dieser kleine Fleck überhaupt als ein Chromosom aufzufassen ist. Wäre dies nicht der Fall, so hätten wir es demnach mit einem unpaarigen *X*-Chromosom zu tun.

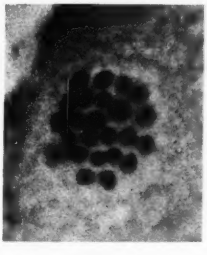


Fig. 46. *Hesperia alveus* Hb. Spermatozytenplatte I mit 24 Chromosomen.

2. In diesem Ei liegen beide Platten in einem Schnitt und eine Eliminationsplatte fehlt, was die Identifizierung der homologen Chromosomen erleichtert. In der oberen Platte kann man einwandfrei 29 Chromosomen zählen, in der unteren dagegen nur 28. Zwei in der oberen Platte nebeneinander liegende Chromosomen werden in der unteren von einem einzigen vertreten, das jedoch fast ebenso gross ist wie die beiden zusammen. Nun liegt aber das untere grosse Chromosom so, dass man es von der Seite sieht und der Spalt sichtbar ist, was vielleicht dazu beiträgt, das Chromosom erheblich grösser erscheinen zu lassen, als es eigentlich ist.

3. Das dritte Ei erinnert mehr an das erste. Hier sind zwar beide Platten vom Messer geteilt worden, aber das Fehlen des Eliminationschromatins und die vollständig kongruente Lage sämtlicher Chromosomen macht die Identifizierung derselben äusserst leicht. In beiden Platten kann man 29 Chromosomen zählen, wobei aber ein grosses und deutliches Chromosom der unteren Platte in der oberen nur durch ein ganz kleines und helles vertreten ist, über dessen Natur als Chromosom man gewisse Zweifel hegen kann.

In drei Eiern konnte ich also eine Verschiedenheit in den beiden Platten nach der ersten Reifeteilung beobachten. Sie ist aber nicht der Art, dass ich mir ein endgültiges Urteil über sie erlauben möchte. Das Material ist zu gering und es hängt ganz vom Zufall ab, ob man gut getroffene Anaphasen erhält. Unter solchen Umständen schien mir die Beschaffung und Untersuchung von neuem Material kaum lohnend, besonders nachdem die drei zuletzt geschnittenen Ovarien nichts prinzipiell neues enthielten. Die Weibchen dieser Art legen ihre Eier nicht leicht in der Gefangenschaft ab, und das Schneiden der Imagoovarien ist mühsam und äusserst zeitraubend, wozu noch kommt, dass der Erfolg höchst unsicher ist.

Hesperia alveus. — Von dieser ziemlich seltenen Art vermochte ich nur ein Weibchen und ein Männchen zu erbeuten.

Der Testis enthält nur drei Platten der ersten Reifeteilung, alle mit 24 Chromosomen (Fig. 46). Alle Chromosomen sind von erheblicher Grösse, und eines von ihnen überragt die übrigen bedeutend der Grösse nach.

Das Ovarium weist 5 Platten der ersten Reifeteilung auf, in denen die gleiche Zahl 24 festgestellt wurde. Auch hier fällt ein Chromosom durch seine bedeutende Grösse auf.

H. malvæ. — Mehrere geschnittene Testes von ganz frischen Imagines enthielten lauter Spermien.

In 7 Oozyten von zwei Weibchen konnte die Chromosomenzahl ganz genau

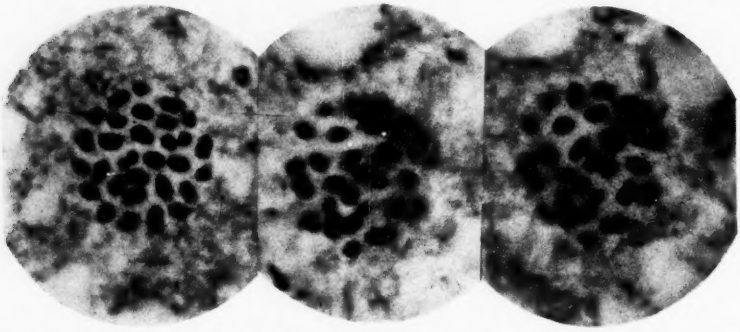


Fig. 47. *Hesperia malvæ* L. Zwei Oozytenplatten mit 31 Chromosomen, eine in zwei Aufnahmen.

bestimmt werden. Sie beträgt *31*. Kein auffallend grosses Chromosom kommt vor, wohl aber ziehen etwa drei Chromosomen durch ihre geringe Grösse (Fig. 47) die Aufmerksamkeit auf sich.

Wenn in der obigen Beschreibung der Arten nichts vom Fundort derselben erwähnt ist, so sind die Exemplare von mir auf der grossen Insel Sarvsalö in der Lill-Pernå Bucht erbeutet worden.

ALLGEMEINE ERÖRTERUNGEN.

Der Verfasser ist sich der Mängel der obigen Untersuchung klar bewusst. Sie kann weder als eine Schilderung der Gametogenese noch als eine Beschreibung der Karyotypen der Rhopaloceren gelten. Die Karyotypen kommen ja bekanntlich immer am deutlichsten in den somatischen Mitosen zum Vorschein, und gerade diese sind von mir nicht untersucht worden. Ausserdem lässt das benutzte Fixiermittel, das Gemisch von CARNOY, bei all seinen Vorzügen, die Morphologie der Chromosomen nicht zu ihrem Rechte kommen. Es schien mir jedoch nicht der Mühe wert, eine derartige allen Ansprüchen genügende

Karyologie der Rhopaloceren anzustreben, denn die Erfahrungen meiner Untersuchungen über andere Lepidopterenfamilien haben mich davon überzeugt, dass die somatischen Chromosomen der Schmetterlinge überhaupt ihrer Form nach wenig charakteristisch sind. Nur ausnahmsweise kommen vereinzelte grosse Chromosomen von besonderer Form vor. Es dürfte nur äusserst selten möglich sein, unter den zahlreichen kleinen Chromosomen von mehr oder weniger kurzzylindrischer Form eines Chromosomensatzes ein bestimmtes Chromosomindividuum zu identifizieren. Hierzu kommen noch praktische und technische Schwierigkeiten, die mit der Beschaffung des nötigen Materials verbunden sind.

Bei den Schmetterlingen kann man die somatischen Mitosen eigentlich nur während der Bildung des Blastoderms studieren, und diese findet bei den verschiedenen Arten zu sehr verschiedener Zeit statt und ist dazu noch von sehr kurzer Dauer. Man kann sich also das nötige Material nur derweise beschaffen, dass man Eier ablegende Weibchen in Gefangenschaft hält und genau den Zeitpunkt der Eiablage notiert und sodann nach bestimmten Zeitperioden die Eier fixiert. Hierbei wird man die wenig erfreuliche Erfahrung machen, dass ein sehr grosses Material vergeblich untersucht werden muss, ehe man über die gewünschten Stadien verfügt.

Die Fixierung bereitet ebenfalls Schwierigkeiten. Als für die somatischen Chromosomen geeignete Fixiermittel werden in erster Linie diejenigen mit Osmiumsäure empfohlen; sie sind aber in unserem Falle völlig unbrauchbar. Die Eier lassen sich nämlich nach einer solchen Fixierung nicht schälen, sondern zerbröckeln und können sogar in ein feines Pulver zerfallen. Ungeschälte abgelegte Eier wiederum, deren Chorion an der Luft erhärtet ist, lassen sich nicht schneiden. Die anderen Fixierungsgemische, die sich besonders für somatische Chromosomen eignen sollen und allgemein von den Botanikern benutzt werden, dringen wieder so langsam und schlecht ein, dass die Chromosomen ganz miserabel fixiert werden und von ihren »Constrictions» überhaupt nichts zeigen. Ich bin schliesslich immer wieder zu dem alterprobten für Insekten besonders günstigen Gemisch von CARNOY (6 : 3 : 1) zurückgekehrt. Ich lasse es aber nicht länger als einige Stunden wirken und wasche die Präparate in einem Gemisch von Chloroform und absolutem Alkohol aus, wonach sie durch reines Chloroform in Parovax eingebettet werden.

Obwohl also die vorliegende Untersuchung durchaus nicht als eine Karyologie der Rhopaloceren charakterisiert werden kann, dürfte sie

trotzdem in zytologischer Hinsicht nicht ohne Interesse sein. Zwar ist die Form der Chromosomen bei den Schmetterlingen überhaupt im grossen und ganzen wenig interessant, und besonders in den Reifeteilungen treten die Chromosomen fast ausschliesslich in sphärischer oder elliptischer Form auf. Wir dürfen demnach keine Resultate erwarten, die mit den von den russischen Botanikern an verschiedenen Pflanzenfamilien gewonnenen Ergebnissen verglichen werden könnten. Ich erinnere nur an die schönen Analysen von NAWASCHIN an *Crepis*-Arten, SVESHNIKOVA an *Vicia*-Arten und die Untersuchungen über die Morphologie der Chromosomen von LEVITSKY (1931). Bei den Schmetterlingen sind ähnliche Analysen an miteinander verwandten Arten nicht oder nur ausnahmsweise möglich. Wir müssen uns hier in erster Linie auf die Zahl- und Grössenverhältnisse der Chromosomen beschränken. Es wird sich indessen zeigen, dass man auch bei den Rhopaloceren gewisse für die Familien charakteristische Karyotypen feststellen kann, obwohl sie nicht so ausgesprochen sind wie bei den Pflanzen.

ZAHL, GRÖSSE UND FORM DER CHROMOSOMEN.

DIE CHROMOSOMENZAHL.

Die Aufgabe, eine zusammenfassende und übersichtliche graphische Darstellung der bei den 67 untersuchten Rhopaloceren-Arten gefundenen Chromosomenzahlen zum Zweck einer vergleichenden Behandlung derselben zu geben, bereitet gewisse Schwierigkeiten.

Erstens haben die Geschlechter derselben Art nicht selten verschiedene Chromosomenzahlen, welche Verschiedenheiten jedoch nicht mit dem Vorkommen von Geschlechtschromosomen verbunden sind, sondern von verschiedenartiger Fusion resp. Fragmentierung der Chromosomen in den beiden Geschlechtern bei der Gametogenese abhängig sind. In solchen Fällen habe ich immer die grössere Zahl als die für die Art charakteristische angegeben.

Zweitens kommen Individuen desselben Geschlechts mit verschiedenen Chromosomenzahlen vor. Hier habe ich mich bemüht, soweit es mir möglich war, festzustellen, welche Zahl als die häufigste angesehen werden kann, und sodann habe ich diese in die graphische Darstellung eingeführt.

Drittens stösst man auf Individuen, die in ein und derselben Gonade, in der Regel in dem Testis, eine ganze Serie von Chromosomen-

zahlen aufweisen. In solchen Fällen habe ich auch die allgemeinste Zahl der Statistik zu Grunde gelegt.

Einige Beispiele mögen die Schwierigkeiten erläutern.

In der Familie der *Pieriden* haben sich die Schwierigkeiten gehäuft, indem nicht nur die beiden Geschlechter verschiedene Zahlen aufweisen, sondern die Zahl noch überdies in demselben Geschlecht wechselt, wobei ein und dasselbe Individuum eine relativ konstante Zahl zeigt, oder aber die Zahl in den verschiedenen Spermatozyten desselben Testis erheblich schwanken kann. So hat z. B. das Männchen von *Leptidia sinapis* 26—28 Chromosomen, das Weibchen dagegen 30—31, vielleicht sogar noch mehr (Fig. 8). Bei *Colias palæno* fanden wir wiederum in dem Testis eines Männchens 31—34 Chromosomen, bei den zwei untersuchten Weibchen dagegen nur die Zahl 31 (Fig. 9).

Bei den *Nymphalinen* hat bei einigen Arten in den Oozyten I eine Fusion von zwei Chromosomen stattgefunden, so dass z. B. bei *Argynnis niobe*, *A. adippe* und *A. paphia* (Fig. 24—26) regelmässig beim Männchen 29, beim Weibchen meistens nur 28 Chromosomen in den Gametozyten I gezählt werden. Bei *Arg. pales* v. *arsilache* scheint die Fusion nicht immer vollzogen zu werden, so dass man für das Männchen 30, für das Weibchen 29 und 30 als die charakteristische Zahl angeben muss. Bei einzelnen *niobe*-Weibchen unterbleibt die Fusion gleichfalls.

Unter den *Lycæniden* entdeckten wir wieder ein zu dem bei den *Argynnis*-Arten beschriebenen umgekehrtes Verhältnis, indem bei *Lycæna astrarche* (Fig. 40) das Männchen nur 23 Chromosomen (unter diesen ein sehr grosses) besitzt, das Weibchen dagegen 24. Bei *Lycæna icarus* sehen wir wiederum eine andere Eigentümlichkeit. Hier ist in der Oozyte I das grösste Chromosom immer mit einem kleineren verbunden, aber die Fusion ist hier nicht bei allen Individuen so innig, dass man nicht die beiden fusionierten Chromosomen deutlich als zwei erkennen könnte.

Unter den oben beschriebenen, bei den Rhopaloceren herrschenden Verhältnissen kann man es gewissermassen als eine Geschmacksache bezeichnen, wie man die graphische Darstellung der Chromosomenzahlenverhältnisse gestalten will. Eine allzu grosse Verschiebung der Zahlenreihen würde indessen kaum hervorgerufen, wenn man anderen als den von mir gewählten Massregeln Folge leisten würde. Im grossen und ganzen würden die Diagramme ihre charakteristischen Eigenschaften trotzdem beibehalten.

Betrachten wir nunmehr nach den vorangegangenen Erklärungen die auf S. 440 wiedergegebenen graphischen Darstellungen (Dia-

gramm I), so entdecken wir, dass sie nicht ohne Interesse sind. Wir fangen unsere Analyse mit den Familien an.

Die drei *Papilioniden* mit 29, 30 und 32 Chromosomen sind hier nicht besonders dargestellt.

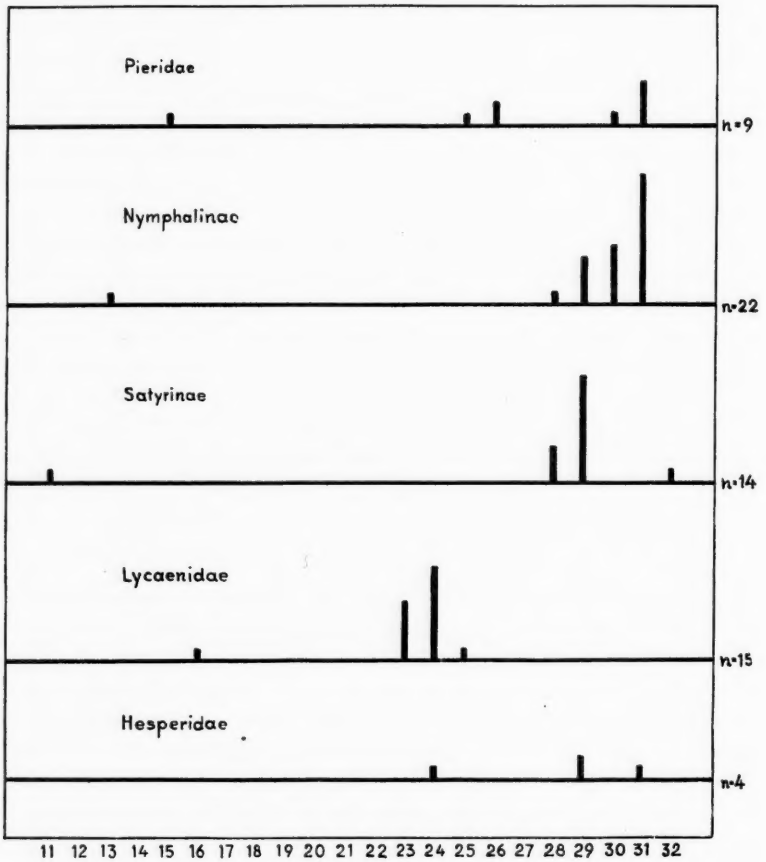


Diagramm I.

Von den neun untersuchten *Pieriden* fallen fünf auf die Klassen 30—31, drei auf die Klassen 25—26, und eine einzige Art *Pieris brassicæ* hat nur 15 grosse Chromosomen.

Unter den 22 *Nymphalinen* fallen 20 auf die Klassen 29—31, eine Art hat 28 Chromosomen und *Argynnis ino* zeigt die niedrige Zahl 13,

wobei aber zu bemerken ist, dass die Chromosomen sehr gross sind.

Die 14 *Satyrinen* verteilen sich auch ähnlich wie die Arten der vorigen Familien, indem 12 Arten zu den Klassen 28—29 gehören, eine Art 32 Chromosomen besitzt und *Erebia medusa* 11 riesengrosse Chromosomen hat.

Bei den *Lycæniden* ist der Höhepunkt der Frequenzkurve nach links verschoben, so dass von den 15 Arten 13 auf die Klassen 23—24 entfallen, nur eine Art 25 Chromosomen hat, und *Zephyrus betulæ* etwa 16 grosse Chromosomen aufweist.

Die vier *Hesperiden* sind nur deswegen graphisch dargestellt, weil sie eine gewisse Ähnlichkeit mit den übrigen Familien zeigen. *Hesperia alveus* mit ihren 24 Chromosomen steht auch hier ziemlich weit links von den drei übrigen mit ihren 29 und 31 Chromosomen.

Es wird, wenn man die Diagramme betrachtet, sofort klar, dass sie gewisse gemeinsame Charakteristika besitzen. In allen Familien zeigt die Verteilung der Arten auf die verschiedenen Klassen eine gewisse Ähnlichkeit. Alle Diagramme besitzen einen mehr oder weniger ausgesprochenen Gipfel, der bei den Pieriden und Nymphalinen bei 31 liegt, bei den Satyriden und Hesperiden (wenn sie überhaupt mitgezählt werden sollen) bei 29 und bei den Lycæniden etwas mehr nach links bei 24. Sämtliche Familien sind aber auch durch eine Spezies charakterisiert, die eine weit geringere Zahl von Chromosomen aufweist, und diese sind immer sehr viel grösser als bei den übrigen Vertretern der Familie.

Durchmustern wir nun das neueste Verzeichnis über Chromosomenzahlen bei Lepidopteren von MAKINO, der hauptsächlich auf BELIAJEFF baut, so finden wir, dass die oben angeführten Rhopaloceren-Familien in ihrer Art durchaus nicht alleinstehend sind. Es gibt auch andere Familien, die eine ganz ähnliche Verteilung der Arten in bezug auf die Chromosomenzahl zeigen. Ich führe hier die Zahlenreihen der 10 Saturniiden und der 15 Geometriden an.

Saturniiden: 13, 19, 29, 30, 30, 30, 31, 31, 33, 49

Geometriden: 13—14, 28, 30, 30, 31, 31, 31, 31, 32, 32, 33, 37, 51, 56, 112

Also wiederum ein ausgesprochener Gipfel bei 30—31 und eine Art mit einer sehr niedrigen Zahl 13 (unter den Saturniiden dazu noch eine mit der Zahl 19).

Ausserdem möchte ich noch die Aufmerksamkeit auf vier Familien lenken, in denen die Kurve der Chromosomenzahlen eine äusserst

geringe Breite hat und nur 2—4 Klassen umfasst. Es sind die folgenden:

8 Sphingiden	27—29	Chromosomen
7 Lasiocampiden	30—31	»
9 Noctuiden	29—31	»
7 Arctiiden	28—31	»

Nur in zwei Familien ist die Variationsamplitude eine weite und die Verteilung der Arten auf der Kurve gleichmässiger.

Notodontidæ: 21, 23, 28, 29, 29, 30, 30, 31, 49

Lymantriiden: 11, 14, 23, 28, 28, 30, 30, 31, 87

Man fragt sich: liegt hier nur ein Zufall vor oder ist diese höchst auffallende Verteilung der Chromosomenzahlen der Ausdruck eines Prozesses, der eine Fusion der Chromosomen verursacht? Es scheint mir, dass wir es tatsächlich mit einer Mutation zu tun haben, die eine Verschmelzung der Chromosomen zu grösseren Verbänden hervorruft. Für eine solche Annahme spricht zunächst die schon hervorgehobene erhebliche Grösse der Chromosomen bei den Arten mit einer geringen Zahl. Man vergleiche z. B. die 11 Riesenchromosomen von *Erebia medusa* mit den 28 von *Erebia lappona*, oder die 12—13 Chromosomen von *Argynnis ino* mit denjenigen der übrigen Arten dieser Gattung. Der Vergleich zwingt, meiner Ansicht nach, zu der Annahme, dass wir es bei den genannten Arten mit wenigen, grossen Chromosomen, mit *Sammelchromosomen* zu tun haben, wie solche ja auch anderwärtig im Tierreich bekannt sind. Ich erinnere an das klassische Beispiel *Ascaris megalocephala*. Wir finden jedoch auch viel näher liegende Beispiele einer solchen Fusion von Chromosomen. Ich verweise zunächst auf den S. 399 erwähnten Fall bei *Lymantria monacha* und füge noch die von SEILER (1922) untersuchten und genau analysierten Verhältnisse bei *Solenobia pineti* hinzu. Bei dieser Art fand SEILER sowohl in der Oogenese als auch der Spermatogenese in den Gametozyten I 30, 31 und 32 Chromosomen. In der Regel enthält ein und dasselbe Individuum nur eine einzige Anzahl, nur bei vereinzelten Weibchen konnten die Eier verschiedene Zahlen aufweisen. Auch die somatischen Chromosomenzahlen konnten an Blastodermmitosen genau festgestellt werden und erwiesen sich als 61, 62 und 63. Die Zahl 64 kam nicht vor, 60 auch nicht (in der Tabelle wird diese Zahl jedoch vier Mal angeführt, obgleich sie dem Text nach fehlen soll). Wenn alle Gameten miteinander fertile Kombinationen bilden, so hätte man auch die Zahlen 60 und 64 erwartet. SEILER erklärt ihr Fehlen damit, dass diese

Kombinationen mit der Höchst- und Mindestzahl so selten sind, dass sie in seinem verhältnismässig kleinen Material nicht realisiert wurden. Was uns in dieser Darstellung der Chromosomenverhältnisse bei *Solenobia pineti* besonders interessiert, ist die Feststellung, dass diese Art ein Chromosom besitzt, dass als ein einheitliches Chromosom oder als zwei oder drei selbständige Chromosomen auftreten kann, sowie dass diese verschiedenen Koppelungsverhältnisse der Chromosomen erblich bedingt sind und sich mendelistisch vererben. Dabei dominiert der eine Typus immer über den anderen. Auf SEILERS in mancher Hinsicht interessanten Darlegungen über die Bedeutung dieser eigenartigen Verhältnisse für den Faktorenaustausch brauchen wir hier nicht näher einzugehen.

Nach meinen Untersuchungen, die ja nur Stichproben von verschiedenen Arten sind, will es mir scheinen, dass *Solenobia pineti* als eine Art mit einer Anzahl verschiedener Chromosomenrassen nicht allein dasteht. Es kommen offenbar viele andere Arten vor, die ähnliche Verhältnisse aufweisen, sonst hätte ich wohl kaum in meinem Material so viele Beispiele finden können.

Auch bei *Phragmatobia fuliginosa* kommen, wie bereits erwähnt, nach den Untersuchungen SEILERS, mehrere Rassen vor, die nur an den Chromosomen unterschieden werden können. Bei einer von ihnen gibt es ein sehr langes Chromosom, das bei einer anderen auf zwei selbständige Chromosome verteilt ist.

Ob in den von SEILER untersuchten Fällen die Entwicklung in der Richtung einer Vermehrung der Chromosomen, d. h. einer Fragmentierung derselben oder umgekehrt in der Richtung einer Verminderung der Chromosomenzahl, also einer Fusion schreitet, darüber äussert sich SEILER mit grosser Vorsicht. Er lässt die Frage offen.

Es gibt aber auch andere Indizien dafür, dass die grossen Chromosomen Sammelchromosomen sind. Schon 1913 beschrieben DONCASTER und HARRISON die Chromosomenverhältnisse bei *Biston hirtarius* und *zonarius* sowie bei dem Bastard zwischen diesen beiden Arten. *Biston hirtarius* ist eine Art, die in zwei verschiedenen Chromosomenrassen auftritt, in einer mit 14 und einer mit 13 Chromosomen. Die letzterwähnte Rasse zeigt deutlich, dass ein Chromosom aus zweien zusammengesetzt ist. Bei den reziproken Bastarden zwischen *hirtarius* und *zonarius* können die Elternchromosomen infolge ihrer verschiedenen Grösse leicht unterschieden werden, und in den meisten Spermatozyten ist es möglich zu konstatieren, dass keine oder nur ganz wenige *zonarius*- und *hirtarius*-Chromosomen miteinander konjugiert haben.

Es kommen aber auch vereinzelte Spermatozyten vor, in denen die Chromosomenzahl nur 50 oder etwas mehr beträgt. Hier haben also zwei oder mehrere *zonarius*-Chromosomen mit einem *hirtarius*-Chromosom konjugiert, sonst wäre eine Abnahme der Chromosomenzahl unter 56 nicht möglich, wenn man nicht bei *zonarius* Autosyndese annimmt. Dass zwei kleinere Chromosomen mit einem grösseren konjugieren spricht aber dafür, dass dieses ein Sammelchromosom ist. Wir können es also als höchst wahrscheinlich ansehen, dass die 14 grossen *hirtarius*-Chromosomen durch eine Fusion von mehreren kleinen Chromosomen von *zonarius*-ähnlichem Typus entstanden sind, sonst könnte kaum eine Affinität zwischen einem *hirtarius*-Chromosom und zwei oder mehreren *zonarius*-Chromosomen vorhanden sein.

Zu diesem Beispiel kann ich einen Fall hinzufügen, der noch deutlicher für die Richtigkeit der Annahme einer Fusion von Chromosomen spricht. Der Fall ist noch nicht vollständig klargelegt und deshalb nicht veröffentlicht. Es handelt sich um eine Kreuzung der schon in der Einleitung berührten Arten *Dicranura vinula* mit 21 Chromosomen mit der in Marocko fliegende *D. delavoiei* mit 31 Chromosomen. Bis jetzt habe ich nur einen Testis des Bastards untersuchen können; die weiblichen Puppen haben überhaupt noch keine Falter ergeben, sondern überwintern zum zweiten Male, wie dies bei den *Dicranura*-Arten gewöhnlich ist. Die Spermatogenese ist aber höchst interessant. Eine nicht ganz geringe Zahl der Spermatozyten zeigt nämlich nur 21 Chromosomen, und sehr zahlreiche Platten der ersten Reifeteilung haben eine Chromosomenzahl, die nur um wenige Chromosomen die Zahl 21 übersteigt. Hier haben also zweifellos von den 31 *delavoiei*-Chromosomen zwei oder mehrere mit einem *vinula*-Chromosom konjugiert. Es dürfte also kaum allzu kühn sein, aus diesem Verhältnis die Schlussfolgerung zu ziehen, dass die *vinula*-Chromosomen Sammelchromosomen sind, die durch Fusion mehrerer Chromosomen von *delavoiei*-ähnlichem Typus entstanden sind.

In diesem Zusammenhang möchte ich auch noch an den S. 398 erwähnten Fall erinnern, in dem durch eine Kreuzung zweier *vinula*-Rassen, beide mit 21 Chromosomen, ein Bastard mit 20 Chromosomen entstand. Hier wird also die Fusion durch eine Neukombination von Genen ausgelöst (FEDERLEY, 1937).

Wir sind also zu der Schlussfolgerung gelangt, dass ein bestimmter Erbfaktor, oder vielleicht mehrere solche, für die Bildung von Sammelchromosomen verantwortlich sind. In einer solchen Annahme liegt nichts unwahrscheinliches. Wir kennen ja schon seit langem Gene, die

die Form der Chromosomen beeinflussen. Solche sind von LESLEY und MANN bei *Mathiola incana* entdeckt und in bezug auf ihre Wirkungsweise experimentell untersucht worden. SEILER (1925) hat auch ähnliche Gene bei *Phragmatobia fuliginosa* gefunden. Diese Gene haben auf die Form aller Chromosomen dieselbe Wirkung. Es darf also als feststehend angesehen werden, dass es Gene gibt, die sozusagen eine generelle Wirkung auf sämtliche Chromosomen eines Satzes ausüben.

Es ist jedoch auch die Möglichkeit vorhanden, dass Gene existieren, die eine ganz spezielle Wirkung auslösen und nur eine Fusion zweier bestimmter Chromosomen hervorrufen, wogegen sie in bezug auf die übrigen Chromosomen völlig wirkungslos sind. In dem deskriptiven Teil dieser Untersuchung sind mehrere Beispiele dafür erwähnt, dass sich zwei nahe verwandte Arten nur dadurch unterscheiden, dass die eine ein Chromosom mehr besitzt als die andere, und dass die Art mit der geringeren Zahl ein besonders grosses Chromosom hat. Es wurde auch die Vermutung ausgesprochen, dass dieses grosse Chromosom durch Fusion zweier kleinerer entstanden wäre. Bei den *Argynnis*-Arten hatten wir Beispiele dafür, dass die beiden Geschlechter mehrerer Arten einen solchen Unterschied zeigen. In einigen Fällen konnte man sogar in dem grossen Chromosom ein Doppelchromosom erkennen, denn es wies eine tief einschneidende Furche auf. Eine Art besass sogar noch Weibchen von zwei Typen, nämlich solche mit zwei Chromosomen und solche mit einem einzigen. Hier können wir also nicht daran zweifeln, dass tatsächlich eine Fusion zwischen zwei Chromosomen stattgefunden hat, und in anderen Fällen werden wohl die Verhältnisse die gleichen sein.

Wie vorsichtig man jedoch bei der Aufstellung ähnlicher Hypothesen sein muss, zeigt in klarer Weise der Fall beim Roggen. Die haploide Chromosomenzahl bei den meisten Roggenrassen ist 7. Es gibt aber auch Rassen mit 8 Chromosomen. Da 7 die für die meisten Gräser charakteristische Grundzahl der Chromosomen ist, so wurde von vielen Zytologen angenommen, dass die Rassen mit 8 Chromosomen durch Fragmentierung eines der 7 Chromosomen der gewöhnlichen Rassen entstanden seien. Ein Vergleich der Grösse der Chromosomen der beiden Rassen sprach ebenfalls für diese Annahme, denn die 8-chromosomige Rasse hatte ein Paar Chromosomen von geringerer Grösse als diejenigen der 7-chromosomigen.

Durch Benutzung verfeinerter Fixierungsmethoden, die die Einschnürungen der Chromosomen deutlicher hervortreten liessen und demzufolge eine sichere Identifizierung der einzelnen Chromosomen der

beiden Roggenrassen ermöglichte, gelang LEVITSKY (1930) der Nachweis, dass die Vermutung, dass bei der älteren 7-chromosomigen Rasse ein Chromosom durch Querteilung in zwei zerfallen sei, nicht richtig ist. Die kleinen Chromosomen der 8-chromosomigen Rasse lassen sich durchaus nicht mit einem grossen der 7-chromosomigen identifizieren.

Es ist also sehr gut möglich, dass z. B. das grosse Chromosom der Art *Argynnis selene* mit der Zahl 30 nicht zwei kleineren der Art *euphrosyne* mit der Zahl 31 entspricht. Da die Chromosomen der Lepidopteren auch in den somatischen Zellen kurz und zylindrisch sind, dürfte es kaum möglich sein die Frage hier endgültig zu beantworten.

Dass aber bei den Insekten durch Mutation eine Fusion zweier Chromosomen hervorgerufen werden kann, zeigt der bekannte von LILIAN MORGAN entdeckte Fall von »attached X-chromosomes» bei *Drosophila melanogaster*. Zwar handelt es sich hier um zwei identische Chromosomen des diploiden Satzes, es ist jedoch durchaus nicht unwahrscheinlich, dass eine solche Bindung zwischen zwei bivalenten, nicht homologen Chromosomen stattfinden könnte, denn eine solche Fusion wird für die Existenz der Art weniger gefährlich, da sie keine durch Non-disjunction hervorgerufene Störung der Harmonie des Genoms verursacht.

Bei einer anderen *Drosophila*-Art finden wir ein Beispiel von Fragmentierung eines Chromosomenpaares. FROLOWA hat nämlich eine in Russland lebende Rasse von *Dr. obscura* gefunden, die nur 4—5 % Männchen hat und sich ausserdem dadurch auszeichnet, dass ein bei der amerikanischen Rasse vorkommendes langes Chromosomenpaar mit einer submedialen Einschnürung durch zwei stäbchenförmige Chromosomenpaare ersetzt ist. Die amerikanische Rasse hat also 5, die russische dagegen 6 Paare Chromosomen. FROLOWA nimmt an, dass die russische Rasse durch Fragmentierung des genannten Chromosomenpaares der amerikanischen entstanden sei.

Auch in bezug auf die Lepidopteren können wir auf eine Untersuchung hinweisen, die klar und eindeutig beweist, dass es innerhalb einer Spezies Rassen gibt, die sich bloss durch verschiedene Chromosomenzahlen unterscheiden. PAULINE DEDERER hat mehrere gezüchtete Stämme von der Saturniide *Philosamia cynthia* auf ihre Chromosomenverhältnisse untersucht und dabei entdeckt, dass die meisten Familien, nämlich deren 29, 13 Chromosomen in den Reifeteilungen aufwiesen. Drei Familien hatten nur 12 Chromosomen, zwei hatten 12, 13 und 14, und eine Familie schliesslich hatte 12 und 13. Nach DEDERER sind in den Familien mit 12 Chromosomen zwei Chromosomen der 13-chromoso-

migen Art gekoppelt und zwar nur in den Spermatozyten erster Ordnung. Denn die Blastodermzellen dieser Rasse enthalten immer 26 Chromosomen. Auch die Familien mit 14 Chromosomen in der ersten Reifeteilung der Spermatogenese zeigen die Chromosomenzahl 26 in den somatischen Zellen. Es dürfte also klar sein, dass bei dieser Art sowohl eine Fusion als auch eine Fragmentierung von einzelnen Chromosomen stattfinden kann.

Über die Chromosomenverhältnisse bei zwei Rassen der oben behandelten Art hat neuerdings KAWAGUCHI interessante Beobachtungen veröffentlicht. KAWAGUCHI bestätigte zunächst die Angaben DEDERERS, dass *Philosamia cynthia Walkeri* FELDER, eine kontinentale Rasse, in den Spermatozyten I und II 13 Chromosomen aufweist. Dagegen hat die in Japan heimische *Ph. cynthia Pryeri* BUTLER immer 14 Chromosomen. Also wieder ein Beispiel dafür, dass zwei einander nahestehende Rassen verschiedene Chromosomenzahlen besitzen. Nach den Abbildungen KAWAGUCHIS zu beurteilen, dürfte hier kaum von einer Fusion resp. Fragmentierung die Rede sein, denn die Chromosomen zeigen keine auffallenden Grössenunterschiede. Das interessante mit diesen Rassen ist jedoch, dass der Bastard zwischen diesen nur 12 Chromosomen hat, und dass unter diesen ein sehr langes mit vier Anschwellungen und ein birnenförmiges vorkommen. In dem erstgenannten sieht KAWAGUCHI eine Kette von vier univalenten Chromosomen und in dem letztgenannten ein trivalentes Chromosom, das aus einem kleineren univalenten und einem grösseren bivalenten Chromosom zusammengesetzt ist. Nach KAWAGUCHI sollen diese eigentümlichen Gebilde ihre Erklärung darin finden, dass 1:o eine Translokation von einem Endstück eines Chromosoms stattgefunden hat, und 2:o eine Verdoppelung eines Chromosoms in weit zurückliegender Zeit vorgekommen ist. Diese verdoppelten Chromosomen haben sodann in verschiedene Richtungen mutiert und konjugieren deshalb nicht mehr miteinander. Hierauf deutet eine öfters beobachtete Annäherung zweier Chromosomen während der Diakinese der 14-chromosomigen Rasse. Infolge der Translokation wird wiederum Kettenbildung möglich, wie wir sie bei verschiedenen Pflanzengattungen kennen.

Es kann also kein Zweifel darüber bestehen, dass die Chromosomenzahl sehr bedeutende Fluktuationen aufweist. Andererseits gibt es aber auch Untersuchungen, die den Beweis dafür erbringen, dass die Chromosomenzahl gewisser Schmetterlingsarten ein äusserst konstantes Merkmal ist. So hat GOLDSCHMIDT (1932) bei den von ihm und seinen Schülern untersuchten 39 Rassen von *Lymantria dispar* aus Europa

Nordamerika, Asien und im letztgenannten Weltteil besonders aus den japanischen Inseln nachweisen können, dass alle Rassen dieselbe Chromosomenzahl, nämlich 31, besitzen. Dagegen erwies sich die Grösse der Chromosomen bei den verschiedenen Rassen sehr verschieden, und zwar so, dass die schwachen Geschlechtsrassen die grösseren, die starken dagegen die kleineren besitzen.

YATSU hat die Spermatogenese von 17 Rassen des Seidenspinners *Bombyx mori* untersucht und keine Verschiedenheiten in Zahl und Form der Chromosomen finden können.

FUSION, ASSOZIATION, KONJUGATION, SEKUNDÄRE PAARUNG UND AGGLUTINATION DER CHROMOSOMEN.

Wir haben die Chromosomenzahl bei den Reifeteilungen der Lepidopteren behandelt und wir haben dabei unterstrichen, welche Schwierigkeiten mit der exakten Bestimmung der haploiden Chromosomenzahl in dieser Ordnung verbunden sind. In erster Linie hielten wir uns bei der Frage auf: »Fusion oder Fragmentierung der Chromosomen» und betonten mehrmals, wie schwer, ja unmöglich es oft ist zu entscheiden, welcher von den beiden Prozessen tatsächlich stattgefunden hat. Es gibt indessen auch andere Schwierigkeiten, die unsere Aufmerksamkeit in Anspruch nehmen.

Zunächst kann eine Vergrösserung der haploiden Chromosomenzahl durch *fehlende Konjugation* gewisser homologer Chromosomen vorgetäuscht werden. Es ist klar, dass der Ausfall der Konjugation eine Vergrösserung der haploiden Chromosomenzahl hervorrufen muss. Ein normal bivalentes Chromosom wird durch zwei univalente ersetzt. Da die Chromosomen eines Sortiments bei den Schmetterlingen oft von verschiedener Grösse sind, und die Grössenklassen überdies in der Regel eine Serie bilden und ohne scharfe Grenzen ineinander übergehen, so wird es unmöglich, in einem Satze festzustellen, ob anstatt eines bivalenten Chromosoms zwei univalente vorkommen. Mit anderen Worten, es ist nicht möglich, zwischen fehlender Konjugation und Fragmentierung eines Chromosoms zu unterscheiden. In dem Fall, dass in einem Testis vereinzelte Spermatozyten mit einem überzähligen Chromosom vorkommen, haben wir es wahrscheinlich mit Ausfall der Konjugation zwischen zwei homologen Chromosomen zu tun. Diese gestörte Konjugation braucht nicht mit fehlender Affinität zwischen den Chromosomen in Zusammenhang zu stehen, wie dies bei zahlreichen Bastarden der Fall ist. Es können die Umweltbedingungen sein, die hier störend eingreifen. So ist bewiesen, dass hohe Temperaturen für

die Konjugation hinderlich sind. Auch ist es denkbar, dass die in der Zelle herrschenden rein physiologischen Verhältnisse Störungen im normalen Verlauf der Konjugation hervorrufen können. Über diese Verhältnisse wissen wir so gut wie nichts. Fälle von überzähligen Chromosomen in einzelnen Spermatozyten gehören durchaus nicht zu den Seltenheiten. Durchmustert man sorgfältig einen Testis mit hoher Frequenz der Reifeteilungen, so wird man fast immer einzelne Spermatozyten finden, die ein oder sogar ein Paar überzählige Chromosomen besitzen. Diese spielen selbstverständlich keine Rolle bei der Beurteilung der Chromosomenzahl und der Variationen in derselben. Im beschreibenden Teil dieser Untersuchung sind mehrere solche Fälle erwähnt.

Eine *sekundäre Paarung*, d. h. eine Verbindung von bivalenten Chromosomen, die also schon eine primäre Konjugation vollendet haben, soll nach zahlreichen Botanikern bei den Pflanzen keine seltene Erscheinung sein. Sie wird von den Phytozytologen, besonders von den englischen mit DARLINGTON an der Spitze, als ein Beweis für Polyploidie angesehen. Verbindungen von vier homologen Chromosomen sind nämlich bei sicher tetraploiden Rassen beobachtet worden, und man schloss hieraus, dass in den Fällen, wo Verbindungen von vier Chromosomen vorkommen, Polyploidie vorliegt.

Sehr oft kommt es jedoch vor, dass die bivalenten Chromosomen keine eigentliche Verbindung eingehen, sondern nur Neigung zeigen, sich einander zu nähern. Auch diese Annäherung wird von vielen Zytologen als eine unvollständige sekundäre Paarung angesehen. Dieser Auffassung hat HEILBORN (1936) energisch widersprochen. Er sieht in der gegenseitigen Annäherung gewisser Chromosomen keine verspätete und unvollendete Konjugation zwischen homologen Chromosomen. Nach HEILBORN liegt nur eine rein mechanische Sortierung der Chromosomen der Grösse nach vor. Diese Gruppierung der Chromosomen hat also nichts mit ihren Genen zu tun. HEILBORN will sie deshalb »*Assoziation*», nicht »sekundäre Paarung» nennen. Dass tatsächlich eine mechanische Sortierung der Chromosomen immer vorhanden wäre, scheint mir nicht endgültig bewiesen zu sein. Dass die Chromosomen in der Metaphaseplatte der ersten Reifeteilung in ihrem Verhalten zueinander oft eine bestimmte charakteristische Konfiguration zeigen, kann zwar nicht bezweifelt werden, obgleich offenbar mehrere verschiedene Typen von Konfigurationen möglich sind. Eine Reihe Untersuchungen auf diesem Gebiete sind bekanntlich von den japanischen Zytologen vorgenommen worden.

HEILBORN, der seine Ansicht auf eingehende Studien zahlreicher *Carex*-Arten stützt, meint, dass in dieser Gattung die gleich grossen Chromosomen sich in der Regel parallel gruppieren. Er begleitet seine Darstellung mit zahlreichen Abbildungen. Die Gattung *Carex* zeigt bekanntlich keine Polyploidie und verhält sich also in dieser Beziehung wie die Lepidopteren. Ein Vergleich scheint deshalb motiviert.

HEILBORN hat zweifellos recht, wenn er behauptet, dass bei den von ihm untersuchten *Carex*-Arten gewisse Kräfte dafür sorgen, dass gleich grosse Chromosomen nahe zueinander zu liegen kommen und dass gewissermassen eine Art Assoziation dieser Chromosomentypen zustande kommt. Dies ist aber kein Hindernis dafür, dass bei Arten mit Polyploidie Neigung zu sekundärer Paarung zwischen homologen Chromosomenpaaren vorkommen kann. Bei den Lepidopteren finden wir bei vielen Arten eine *Assoziation bestimmter Chromosomen* von ganz verschiedener Grösse und offenbar mit verschiedenen Genen. In vielen Fällen kommt diese Assoziation einer Fusion sehr nahe. Ich erinnere an das lange Chromosom von *Lycæna icarus*, das in den Oozyten I mit einem ganz kurzen verbunden ist, und an die Verhältnisse bei der Oogenese einiger *Argynnis*-Arten. Hier sind ein grösseres und ein kleineres Chromosom miteinander assoziiert resp. fusioniert. Bei *Arg. arsilache* und *niobe* kommen noch beide Typen von Verbindung oder Annäherung vor, wogegen eine vollständige Fusion bei *adippe* und *paphia* durchgeführt ist. Die eigenartige Kettenbildung bestimmter Chromosomen in der Mitte der Oozytenplatte von *Leptidia sinapis* verdient in diesem Zusammenhang ebenfalls erwähnt zu werden. Ob in den obenerwähnten Fällen ein Austausch von Chromosomenstücken (»Interchange») stattgefunden hat, wie wir sie bei den Oenotheren annehmen, kann selbstverständlich nicht festgestellt werden.

Es fällt auf, dass die besprochenen Assoziationen und Fusionen in den meisten Fällen in den Oozyten entdeckt wurden. Nur in einem Fall, bei *Lycæna astrarche*, wurde in den Spermatozyten ein grosses Chromosom gefunden, während bei den Oozyten kein entsprechendes zu entdecken ist. Anstatt dessen besitzen diese ein Chromosom mehr. Es scheint mir, als wären die Bedingungen in den Oozyten günstiger nicht nur für eine regelrechte Konjugation der homologen Chromosomen, sondern auch für Verbindungen verschiedener Art zwischen nicht homologen Chromosomen. Ich erinnere daran, dass bei vielen Bastarden, sowohl im Tier- als im Pflanzenreich, eine Konjugation zwischen den artfremden Chromosomen in den Oozyten beobachtet wor-

den ist, während eine solche in den Spermatozyten überhaupt nicht stattfindet. Ich möchte weiter darauf hinweisen, dass in der normalen Oogenese der Schmetterlinge ein Stadium vorkommt — es handelt sich um die Metaphase der ersten Reifeteilung, die sich über eine sehr lange Zeit erstreckt — in dem die Chromosomen sehr stark zur Kettenbildung neigen, wie auch SEILER bei seinen Untersuchungen festgestellt hat. Etwas entsprechendes habe ich niemals in der Spermatogenese beobachtet.

Schliesslich möchte ich noch erwähnen, dass bei älteren, überreifen Eiern und bei abgelegten unbefruchteten Eiern die Chromosomen oft zu Ketten vereinigt sind, sowie das schlechte Fixierung Kettenbildung hervorrufen kann. Im erstgenannten Fall handelt es sich offenbar um pathologische Zustände, die eine *Agglutination* der Chromosomen verursachen, im zweiten wiederum um *Artefakte*. Charakteristisch für diese ist jedoch, dass sie nur im weiblichen Geschlecht vorkommen.

CHROMOSOMENZAHL UND KAMPF UM'S DASEIN.

Welche Bedeutung kann man der Chromosomenzahl in selektionstheoretischer Hinsicht beimessen? Ist eine grosse Anzahl im Kampf um's Dasein vorteilhafter als eine kleinere?

Über diese Fragen haben die Botaniker Aufschlüsse zu geben vermocht. Bei den Pflanzen liegen indessen die Verhältnisse anders. Die Untersuchungen der Botaniker gelten in erster Linie einem Vergleich zwischen diploiden und polyploiden Arten. Sie haben feststellen können, dass an den äussersten Grenzen des Verbreitungsgebietes einer Pflanze — es möge sich um hocharktische oder wüstenartige Gegenden handeln — die diploiden Formen selten sind oder ganz fehlen und von polyploiden ersetzt werden. Diese Tatsache ist von grossem Interesse und ihre Erklärung nicht minder interessant. Die polyploiden Rassen mit ihrem doppelt oder mehrfach grösseren Gensatz bieten selbstverständlich weit grössere Möglichkeiten für die Entstehung von Mutationen als die diploiden Typen. Wenn diese Mutationen Selektionswert haben, liegt ausserdem noch die Möglichkeit ihrer Wiederholung in mehreren Chromosomen vor, und es entstehen die bekannten Polymerien, die bei diploiden Rassen ausgeschlossen sind.

Bei den Schmetterlingen können wir zwar nicht mit Polymerien in diesem Sinne rechnen, da Polyploidie hier nicht nachgewiesen ist und, nach allem zu urteilen, überhaupt nicht vorkommt. Man kann sich jedoch auch hier die Frage stellen, ob nicht eine grössere Chromo-

somenzahl gewisse Vorteile mit sich bringe. Je geringer die Koppelungsgruppen sind, um so geringer sind die Kombinationsmöglichkeiten von wertvollen neuen Mutationen, und umgekehrt wäre eine grosse Anzahl Koppelungsgruppen im Kampf um's Dasein ein Vorteil. Wenn diese Betrachtungsweise richtig wäre, könnte man erwarten, dass in einer Gattung die Arten mit einer grösseren Chromosomenzahl eine weitere Verbreitung hätten als diejenigen mit einer geringeren. Wie verhalten sich in dieser Beziehung die Arten der Rhopalocerengattungen, deren Chromosomenzahlen untersucht wurden?

Ich habe die Verbreitung der Tagfalter Finnlands nach dem Verzeichnis von GRÖNBLOM (1936) genau studiert und mit der Chromosomenzahl verglichen, jedoch ohne irgend einen Zusammenhang finden zu können. So kommt *Pieris brassicæ* mit 15 Chromosomen in allen 21 naturhistorischen Provinzen Finnlands vor und ist eine der häufigsten Arten. Die nahen Verwandten *napi* mit 25 und *rapæ* mit 26 Chromosomen haben fast dieselbe Verbreitung, aber *rapæ* ist überall seltener und fehlt in einigen der nördlichsten Provinzen.

Von den 13 untersuchten *Argynnis*-Arten hat *ino* nur 12—13 Chromosomen, *lathonia* dagegen 30, ihre Verbreitung aber ist genau dieselbe. Beide Arten fehlen nur in Kuusamo und nördlich der 68. Breite. *Arg. aphirape* mit 28 und *arsilache* mit 29—30 Chromosomen kommen in allen Provinzen vor; dasselbe ist der Fall mit *freija* mit 31 und *frigga* mit 31 Chromosomen. *Arg. niobe* und *adippe*, beide mit 28 und 29 Chromosomen, sind nicht nördlich der 63. Breite gefunden worden. Es ist durchaus nicht möglich, irgend einen Zusammenhang zwischen Verbreitung und Chromosomenzahl zu finden.

Gehen wir wieder von den rein lappländischen Arten aus, so finden wir unter diesen *Erebia medusa* v. *polaris* mit der kleinsten Chromosomenzahl 11, während die übrigen alle hohe Zahlen besitzen. *Colias hecla* hat 31 wie *Melitæa iduna*; *Arg. thore* v. *scandinavica* hat 30 und von den beiden *Erebia*-Arten haben *disa* 29 und *lappona* 28. Also existiert kein Unterschied zwischen den hochnordischen Arten und den südlicheren in bezug auf die Chromosomenzahl.

Ferner ist den Botanikern der Nachweis gelungen, dass gewisse Beziehungen zwischen der Chromosomenzahl und der Entwicklungsweise der Pflanzen bestehen. Die annuellen Pflanzen sollen in der Regel diploid sein, während die perennierenden Arten im allgemeinen polyploid sind.

Diese interessanten Beobachtungen der Botaniker haben mich dazu angeregt, nach irgend welchen Beziehungen zwischen Chromosomen-

zahl und Lebensweise bei den Schmetterlingen zu suchen. Es ist selbstverständlich, dass solche Beziehungen nur bei Arten innerhalb einer Gattung gesucht werden dürfen. Denn dieselben Chromosomenzahlen finden wir ja häufig bei Arten ganz verschiedener Familien, und hier kann ein Vergleich überhaupt nicht in Frage kommen. In meinem kleinen Material gibt es eigentlich nur zwei Gattungen, *Argynnis* und *Lycœna*, die eine grössere Anzahl enthalten.

Die Arten der Gattung *Lycœna* sind jedoch für die Beantwortung unserer Frage von geringem Wert, da die Chromosomenzahl derselben entweder 23 oder 24 ist. Die nahe verwandte *Cyaniris argiolus* hat die grösste Chromosomenzahl 25 und erscheint im Frühling als erster aller Bläulinge, während *Zephyrus betulæ* mit ca. 16 Chromosomen erst im August und September fliegt. Man könnte sich versucht fühlen, die Vermutung auszusprechen, je grösser die Chromosomenzahl, um so schneller die Entwicklung. Wir fügen jedoch gleich hinzu, dass *Thecla rubi* mit 23 Chromosomen auch schon früh im Mai fliegt.

Wie verhalten sich nun die *Argynnis*-Arten, deren Chromosomenzahl zwischen 28 und 31 schwankt, wenn wir *ino* (n = 12—13) ausser der Rechnung lassen? Die früheste, schon im Mai fliegende Art *freija* hat 31 und die sodann Ende Mai erscheinende *euphrosyne* gleichfalls 31 Chromosomen. *Frigga* (n = 31), *selene* (n = 30), *arsilache* (n = 29—30) und *aphirape* (n = 28) fliegen erst im Juni—Juli. Erst Ende Juli und im August erscheinen die grossen Arten *aglaja* (n = 29) und *adippe, niobe* und *paphia,* alle drei mit 28—29 Chromosomen, sowie *ino* (n = 12—13). *Lathonia* (n = 30) bildet eine Art für sich, indem sie als Imago überwintert und deshalb im Herbst und Frühling fliegt. *Thore* (n = 30) kann auch nicht mit den übrigen Arten verglichen werden, da die Art nur in Lappland vorkommt. Im grossen und ganzen zeigen also auch die *Argynnis*-Arten, dass die Arten mit einer grösseren Chromosomenzahl im allgemeinen eine schnellere Entwicklung durchmachen als diejenigen mit einer kleineren.

Wir wollen jetzt noch die Arten mit einer besonders kleinen Chromosomenzahl mit ihren nächsten Verwandten vergleichen.

Pieris brassicæ (n = 15) erscheint später, erst im Juni, während *napi* (n = 25) und *rapæ* (n = 26) schon im Mai fliegen.

Hesperia alveus (n = 24) fliegt im Juli und August, *malvæ* (n = 31) dagegen im Mai.

Erebia medusa v. *polaris* (n = 11) kann leider nicht mit den übrigen Arten der Gattung verglichen werden, da sie nur im hohen

Norden vorkommt, wo überhaupt fast alle Arten gleichzeitig während des kurzen Sommers fliegen.

Es braucht kaum hervorgehoben zu werden, dass die Zahl der angeführten Fälle bei den Rhopaloceren viel zu gering ist um uns zu überzeugen, dass Chromosomenzahl und Entwicklungsgeschwindigkeit in irgend welchem Zusammenhang stehen. Ich hätte sie kaum angeführt, wenn ich nicht auch in anderen Familien Beispiele derselben Art gefunden hätte.

Bei meinen Kreuzungsversuchen mit den *Pygæra*-Arten war es selbstverständlich von grösstem Gewicht, dass die Arten gleichzeitig ausschlüpften. Ich war infolgedessen gezwungen, die Zeit des Ausschlüpfens genau festzustellen und die sich langsamer entwickelnden Arten zu treiben, um so das gleichzeitige Ausschlüpfen zu erreichen. Es erwies sich nun, dass sich folgende Reihenfolge ergab: *anachoreta* (n = 30), *curtula* (n = 29) und *pigra* (n = 23). *P. anastomosis* (n = 25) hat eine andere Lebensweise — sie überwintert als Raupe — und fällt ausserhalb der Serie. Also wiederum: je grösser die Chromosomenzahl, um so früher das Ausschlüpfen.

In der Gattung *Dasychira* haben die beiden Arten *selenitica* (n = 22) und *pudibunda* (n = 87) einen ähnlichen Lebenszyklus, aber *pudibunda* scheint zu den frühesten Schmetterlingen zu gehören; erst etwas später im Juni erscheint *selenitica*. *D. abietis* (n = 22) hat eine ganz andere Entwicklungsweise, indem sie als Raupe — nicht als Puppe wie die vorgenannten Arten — überwintert.

Von den *Biston*-Arten erscheint *zonaria* (n = 56) schon im Winter, wenn der Schnee noch liegt, während *hirtaria* (n = 14) erst im Mai fliegt.

Die *Orgyia*-Arten erscheinen in folgender Ordnung: *gonostigma* (n = 30) und *ericæ* (n = 30) im Juli, *antiqua* (n = 14) erst im Spätsommer und Herbst. Zwar überwintert *gonostigma* im Raupenstadium und kann deshalb nicht mit den anderen verglichen werden. Aber *ericæ* und *antiqua* verhalten sich ganz ähnlich, indem sie beide im Eistadium überwintern. Ich erinnere daran, dass auch *Zephyrus betulæ* als Ei den Winter überlebt und gleichfalls nur eine geringe Anzahl Chromosomen besitzt.

Selbstverständlich ist die Zahl der angeführten Beispiele zu gering und diese sind auch noch ausgewählt. An und für sich sind sie nicht genügend beweiskräftig; sie schienen mir jedoch interessant zu sein und können zu fortgesetzten Untersuchungen anregen.

CHROMOSOMENZAHL UND PHYLOGENIE.

Wir haben die Frage von der Phylogenie der Chromosomenzahl schon mehrmals gestreift. Hier wollen wir sie etwas eingehender behandeln.

Es ist in der Literatur öfters diskutiert worden, ob eine Tendenz zur Verminderung oder Vermehrung der Zahl der Chromosomen in der Evolution verspürt werden kann. Für eine Gattung ist festgestellt worden, dass die primitiveren Arten zahlreiche Chromosomen besitzen, die hochspezialisierten dagegen eine geringere Zahl, und man hat daraus den Schluss gezogen, dass sich die Evolution in Richtung einer Abnahme der Chromosomenzahl bewege, d. h. dass eine Fusion der Chromosomen stattfinde. In einer anderen Gattung liegen die Verhältnisse dagegen umgekehrt, die am wenigsten differenzierten Arten haben eine kleine Chromosomenzahl, während sich die höchstspezialisierten Arten durch hohe Zahlen auszeichnen. Der Entdecker dieser Verhältnisse ist der Meinung, eine Entwicklungstendenz zu einer Verteilung des Idioplasmas auf kleinere aber zahlreichere Einheiten gefunden zu haben, und glaubt also an eine fortschreitende Fragmentierung der Chromosomen.

Ganz davon abgesehen, dass es nach dem heutigen Standpunkt der Biologie kaum mehr möglich sein dürfte, im allgemeinen zwischen höher und niedriger differenzierten Arten zu unterscheiden — es könnte höchstens die Rede sein von mehr oder weniger stark spezialisierten Organen — ist die Fragestellung falsch. Auch die Veränderungen der Chromosomenzahl sind offenbar eine Folge von Mutationen, und obgleich es nach den Untersuchungen von JOLLOS orthogenetische Mutationen gibt, so ist wohl doch die grosse Mehrzahl der Mutationen richtungslos. Es ist also nicht richtig, in der Evolution *entweder* eine Verminderung *oder* eine Vermehrung der Chromosomen zu sehen, es kommt mit aller Wahrscheinlichkeit *sowohl* eine Verminderung *als auch* eine Vermehrung vor. Für eine solche Auffassung sprechen die neuesten Resultate der *Drosophila*-Forschung. Sie hat Fragmentierungen und Fusionen, Translokationen und Inversionen von Chromosomen entdeckt und gezeigt, dass diese ganz verschiedenartigen Veränderungen vollkommen konstant sind.

In einem vorgängigen Abschnitt haben wir die Fusionen und Fragmentierungen schon eingehend behandelt. Hier möchte ich nun auf Grund der bekannten Chromosomenzahlen bei den Lepidopteren die Bedeutung dieser Zahlen sozusagen vergleichend phylogenetisch in Angriff nehmen.

Betrachten wir die graphische Darstellung der Chromosomenzahlen bei den Rhopaloceren (Diagramm II) und bei den Lepidopteren überhaupt, soweit sie in der Literatur bekannt sind, so fällt sofort auf, dass die Zahlen 29—31 entschieden die häufigsten sind. Zu den Zahlen, die den Diagrammen zugrunde liegen, könnte ich aus meinen noch unveröffentlichten Untersuchungen eine grosse Menge hinzufügen, und

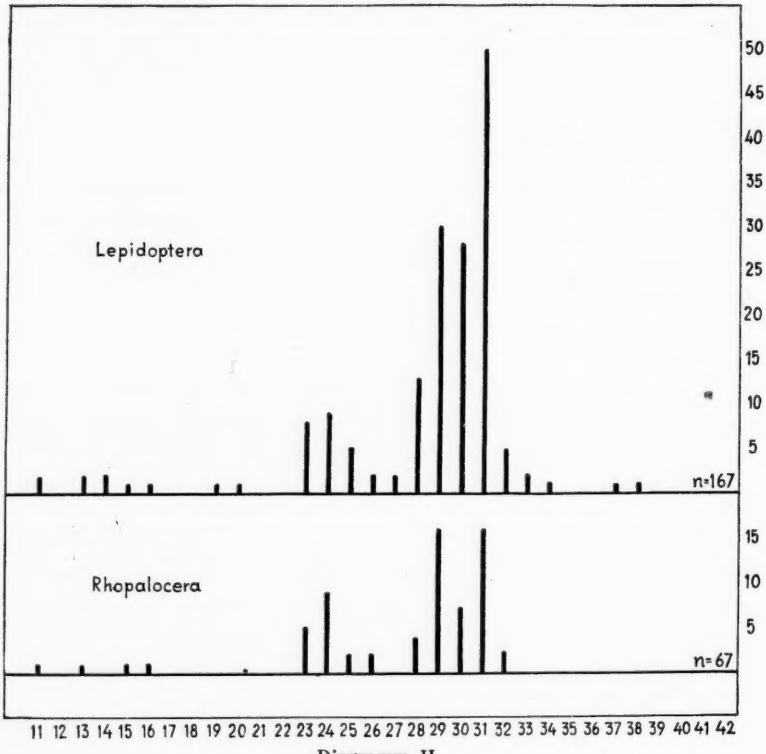


Diagramm II.

diese würden nur dazu beitragen, die Klassen 29—31 zu vergrössern, während der Zuwuchs der übrigen Klassen ganz unbedeutend wäre. Unter den Rhopaloceren bilden die Arten der Klassen 29—31 etwa 58 % der untersuchten Arten und bei allen Lepidopteren steigt ihr Anteil sogar auf 64 %. Der Unterschied erklärt sich dadurch, dass die Familie der Lycæniden mit keiner Art zu den Klassen 29—31 beiträgt, zu den Klassen 23—24 dagegen mit 13. Unter den Nymphalinen

gehören aber von den 22 untersuchten Arten 21 oder 91 % zu den Klassen 29—31.

BELIAJEFF (1930) hat schon in seiner Abhandlung die Aufmerksamkeit darauf gelenkt, dass die Chromosomenzahlen 29—31 bei den Lepidopteren sehr häufig vertreten sind, und glaubt aus dieser hohen Frequenz — wie es mir scheint mit Recht — den Schluss ziehen zu können, dass diese Zahlen die phylogenetisch ältesten sind. Zur Stütze dieser seiner Ansicht führt er die Untersuchung von PCHAKADZE (1930) über die Karyologie der Trichopteren an. Diese Ordnung wird bekanntlich als die den Lepidopteren am nächsten verwandte angesehen, und auch hier sind die Zahlen 29—30 die häufigsten. Von den 24 von PCHAKADZE untersuchten Arten haben 10 oder gegen 42 % 29—30 Chromosomen. Eine höhere Zahl kommt überhaupt nicht vor, die niedrigeren halten sich meistens um 20 herum, die niedrigsten sind 10 und 6.

Eine kritische Prüfung der Chromosomendiagramme ergibt nun weiter, dass die Klassen mit einer höheren Zahl als 31 überhaupt sehr selten sind. Bei den Rhopaloceren gibt es nur eine solche Klasse, diejenige mit 32 Chromosomen, und sie enthält nur 2 Arten. Bei anderen Ordnungen sind die höheren Zahlen häufiger vertreten, obgleich auch hier selten. In dem Diagramm fehlen die Klassen 49, 51, 56 und 87, die alle mit einer Art vertreten sind. Schliesslich hat REGNART bei der Geometride *Phigalia pedaria* FABR. die Zahl 112 gefunden, die als Höchstzahl anzusehen ist.

Wenden wir uns jetzt den Klassen mit niedrigerer Zahl als 29 zu, so finden wir sie weit zahlreicher vertreten und die Artfrequenz ist in diesen auch weit grösser. Diese Klassenverteilung scheint mir auch für die Richtigkeit der schon bei der Behandlung der einzelnen Rhopalocerenfamilien ausgesprochenen Ansicht zu sprechen, dass nämlich Mutationen, die zu einer Fusion von Chromosomen geführt haben, häufig vorgekommen sind. Die Seltenheit der Arten mit höheren Chromosomenzahlen könnte umgekehrt als Anzeichen der Seltenheit von Mutationen, die Fragmentierungen hervorrufen, angesehen werden. Von genetischem Standpunkt würde man zwar, wie schon in anderem Zusammenhang betont wurde, eher erwarten, dass eine Fragmentierung nützlich wäre, da hierdurch die Kombinationsmöglichkeiten von neuentstandenen Genen mit Selektionswert zahlreicher werden. Offenbar haben sich aber zahlreiche Arten mit geringer Chromosomenzahl sowohl bei den Lepidopteren als auch unter den Trichopteren im Kampf um's Dasein mit Erfolg behaupten können. Vielleicht kommt Austausch von Chromosomenteilen in diesen grossen

Sammelchromosomen so häufig vor, dass hierdurch schon genügend Möglichkeiten zu Neukombinationen geboten sind.

CHROMOSOMENZAHL UND GENOM.

Wir sind demnach durch das Studium der Chromosomen bei den Rhopaloceren zum Schlusse gelangt, dass die Zahl der Chromosomen nicht von vitaler Bedeutung ist. Es ist schliesslich das Genom, das in letzter Hand über Leben und Tod entscheidet. Die Art und Weise der Verteilung der Gene auf eine grössere oder geringere Zahl von Chromosomen scheint dagegen eine untergeordnete Rolle zu spielen. Bei der embryonalen Entwicklung dürfte sie jedenfalls ziemlich gleichgültig sein. Die Entwicklung eines Bastards, dessen Eltern ganz verschiedene Chromosomenzahlen aufweisen, kann trotzdem ohne jegliche Störung vor sich gehen. Erst die Bildung der Geschlechtszellen muss als eine kritische Phase bezeichnet werden, und hier scheitert zunächst die regelrechte Konjugation der maternellen und paternellen Chromosomen, was wiederum eine regellose Verteilung der Chromosomen zur Folge hat. Hierdurch entstehen Genome, die entweder keine normale Gameten ergeben oder, wenn dies der Fall wäre, dennoch nicht bei der Befruchtung in einer lebensfähigen Kombination von Genen resultieren.

Einige Beispiele von Kreuzungen zwischen Arten mit bekannten Chromosomenzahlen werden am besten teils die Rolle der Chromosomen, teils diejenige der Gene erläutern.

Die beiden einander sehr ähnlichen Arten *Cerura furcula* ($n = 29$) und *C. bifida* ($n = 49$) lassen sich äusserst leicht kreuzen, wenn *furcula* das Weibchen ist. Die kreuzbefruchteten Eier entwickeln sich sehr gut und ergeben Falter, die äusserlich vollständig normal aussehen. Die Spermatogenese des Bastards ist jedoch sehr stark gestört, und nur ganz vereinzelte Spermien vereinen sich mit den Eiern der Elternarten zu lebensfähigen Individuen. Die meisten der von Bastardspermien befruchteten Eier ergeben überhaupt keine Raupen. Die Bastardweibchen wiederum sind zwar auch phänotypisch völlig normal, besitzen jedoch öfters nur kümmerlich entwickelte Eier. Auch die vereinzelten normal aussehenden Eier enthalten keinen normal entwickelten Kern, sondern nur Chromatinbrocken.

Wir sehen hier ein Beispiel dafür, wie die im Bastard durch das Ei und die Samenzelle der Elternarten zusammengebrachten verschiedenen Chromosomensätze einerseits keine entwicklungsphysiologischen Störungen in der Ontogenie des Bastards hervorrufen, anderseits jedoch in beiden Geschlechtern des Bastards eine normale Keimzellenbildung

verhindern. Beim Männchen wird die normale Konjugation sicher infolge der verschiedenartigen Chromosomensätze der Eltern verhindert und demzufolge die normale Entwicklung von Spermien gestört. Beim Weibchen liegen die Verhältnisse vermutlich etwas anders. Hier sind die Geschlechtsfaktoren der beiden Elternarten wahrscheinlich so disharmonisch, dass die Oogenese einen pathologischen Verlauf erhält.

Anderseits sei hier eine Kreuzung angeführt, in der beide Eltern dieselbe Chromosomenzahl besitzen, die Konjugation bei den reziproken Bastardmännchen ganz normal verläuft und diese, sowie das Weibchen der einen Kreuzung, völlig normal und fertil sind, während das phänotypisch normale Weibchen der reziproken Kreuzung überhaupt keine Eier entwickelt. Es handelt sich um die Bastarde zwischen den beiden Lasiocampiden *Epicnaptera ilicifolia* L. (n = 31) und *E. tremulifolia* HB. (n = 31). Wenn *tremulifolia* die Mutter ist, so sind beide Geschlechter des Bastards fertil. Ist dagegen *ilicifolia* die Mutter, so enthält das riesengrosse Weibchen lauter völlig leere Ovarialfollikel, während das Männchen, wie gesagt, fertil ist. Hier sind es also nicht die Chromosomen als solche, die die Sterilität verursachen, sondern die Geschlechtsgene. Das *ilicifolia Y*-Chromosom bildet mit dem *tremulifolia X*-Chromosom eine disharmonische Kombination, weil die in diesen Chromosomen lokalisierten Geschlechtsgene nicht miteinander harmonisch arbeiten können.

Ein ähnliches Beispiel haben wir in den reziproken Bastarden zwischen den beiden Sphingiden *Metopsilus porcellus* L. (n = 29) und *Chœrocampa elpenor* L. (n = 29). Wenn bei der Kreuzung *porcellus* als Mutterart benutzt wird, so ist der Bastard in beiden Geschlechtern fruchtbar, während in der reziproken Kreuzung das Bastardmännchen, wie zu erwarten ist, völlig fertil ist, das Weibchen dagegen in seiner Entwicklung das Puppenstadium niemals überschreitet. Während also bei den drei fertilen Bastardtypen die Kooperation der artfremden Chromosomen in der embryonalen und postembryonalen Entwicklung sowie bei der Konjugation normal verläuft, ist beim Bastardweibchen *elpenor* × *porcellus* die Kombination von einem *elpenor Y*-Chromosom mit einem *X*-Chromosom von *porcellus* eine subletale Kombination, die die normalen histolytischen und histogenetischen Prozesse in der Puppe paralysieren. Es ist ohne weiteres klar, dass die Chromosomenzahl hier keine Rolle spielen kann. Nur die Gene, und zwar nur die Geschlechtsgene verursachen hier eine Unterbrechung der Metamorphose und rufen so — obgleich erst nach 2—3 Jahren — den Tod hervor. (Vgl. FEDERLEY, 1929 und 1932.)

Es dürfte also ganz klar sein, dass die Chromosomen als Verbände von Genen im Vergleich mit den Genen selbst eine untergeordnete Rolle spielen. Die Art der Verteilung der Gene auf eine bestimmte Anzahl Chromosomen ist keine so konstante und absolute, wie öfters angenommen wird. Fusionen, Fragmentierungen und Translokationen der Chromosomen scheinen weit häufiger zu sein, als man bisher gewusst hat. Solche Veränderungen der Chromosomenzahl und des Chromosomensatzes können vermutlich sowohl durch Mutationen, also Veränderungen in dem Genom selbst, als auch durch peristatische Einflüsse verursacht werden. Die Chromosomenzahl muss also als ein phänotypisches Merkmal charakterisiert werden, obgleich es als solches von relativer Konstanz ist.

FORM UND GRÖSSE DER CHROMOSOMEN.

Von vielen Karyologen ist mit Recht betont worden, dass die Form der Chromosomen weit wichtiger ist als die Zahl. Die Form soll selbstverständlich in erster Linie an somatischen Chromosomen studiert werden. Dies gilt vor allem für die Pflanzen, denn diese bieten in ihren Wurzelspitzen ein wunderbares Material für Chromosomenstudien. Ganz anders liegen die Verhältnisse bei den Lepidopteren. Die besten somatischen Chromosomen finden wir hier in den Blastodermzellen, aber auch hier sind die Chromosomen oft kugelförmig oder im besten Fall stäbchenförmig, jedoch immerhin kurz und dick ohne besonders charakteristische Einschnürungen. Die Form der Meiosischromosomen ist noch weniger charakteristisch. Bei fast allen untersuchten Arten sind die Chromosomen kugelrund oder oval, zuweilen kurz zylindrisch.

Am auffallendsten ist die Entdeckung, dass die Chromosomen von *Oeneis jutta Satelliten* besitzen. Solche sind meines Wissens bei Insekten noch nicht entdeckt worden. Von grösstem Interesse wäre natürlich zu erfahren, ob die nahe verwandten hochnordischen Arten der Gattung auch mit Satelliten ausgestattete Chromosomen haben. Leider dürften die Aussichten, gut fixiertes Material von diesen seltenen Arten zu erhalten, sehr minimal sein.

Die Grössenunterschiede unter den Chromosomen einer Garnitur sind meistens ziemlich gering. Zuweilen kann ein Chromosom die übrigen an Grösse übertreffen und es ist dann wohl durch Fusion zweier Chromosomen von gewöhnlicher Grösse entstanden. Wie vorsichtig man bei der Beurteilung solcher Fälle sein soll, ist bereits betont worden.

Wenn eine Art eine weit geringere Zahl Chromosomen besitzt als

die übrigen Vertreter der Gattung, so sind diese Chromosomen immer sehr erheblich grösser. Das schönste Beispiel in dieser Beziehung bietet uns *Erebia medusa* mit den elf Riesenchromosomen, aber auch *Argynnis ino* und *Pieris brassicæ* illustrieren in schöner Weise die obige Regel. Wir brauchen hier nicht näher auf diese Fragen einzugehen, da sie in anderem Zusammenhang schon eingehend diskutiert worden sind.

Die Untersuchung über die Gametogenese der Schmetterlinge wurde im Jahre 1912 begonnen und dann mit zahlreichen längeren und kürzeren Unterbrechungen an verschiedenen Instituten fortgesetzt. Zunächst wurde das eingesammelte Material im Zoologischen Institut der Universität Helsingfors bearbeitet. In der Kriegszeit während der Jahre 1916—1918 hatte ich als Inhaber des ROSENBERGschen Stipendiums der Universität Helsingfors den Vorzug, im Botanischen Laboratorium der Hochschule zu Stockholm über einen Arbeitsplatz zu verfügen, wodurch mir die Gelegenheit geboten wurde, dort die Bearbeitung des Materials fortzusetzen. Nachdem im Jahre 1923 an der Universität Helsingfors ein Genetisches Institut gegründet worden war, sind die Untersuchungen dort weitergeführt und in bezug auf die Rhopaloceren zu einem gewissen Abschluss gebracht worden.

Es ist mir eine angenehme Pflicht, dem Consistorium academicum der Universität Helsingfors für das mir seinerzeit bewilligte Stipendium sowie meinen Freunden, dem Direktor des Zoologischen Instituts, Helsingfors, Herrn Prof. Dr. ENZIO REUTER, und dem Direktor des Botanischen Laboratoriums, Stockholm, Herrn Prof. Dr. OTTO ROSENBERG, für den mir zu Verfügung gestellten Arbeitsplatz und für das mir stets in liebenswürdigster Weise erwiesene Entgegenkommen meinen aufrichtigen und tief empfundenen Dank auszusprechen.

Bei der Beschaffung des Materials hat sich in erster Linie mein Assistent am Genetischen Institut, Herr Mag. phil. ESKO SUOMALAINEN, meiner Dankbarkeit verdient gemacht. Auf seinen Reisen nach Kusamo, Åland und anderen Gegenden hat er sich stets bemüht, Ovarien und Testes dort vorkommender, seltener Arten zu fixieren. Ausserdem hat er Sammler dazu angeregt, mir lebendige Falter nicht häufiger Arten zuzusenden. Für seine aufopfernde und wertvolle Hilfe spreche ich ihm meinen besten Dank aus. Auch Herrn Mag. phil. ADOLF FR. NORDMAN, der mir in Lappland Material der hochnordischen Arten fixiert hat, bin ich zu grossem Dank verpflichtet.

ZUSAMMENFASSUNG.

Es wurde die Chromosomenzahl 67 finnländischer Tagschmetterlinge in den Reifeteilungen festgestellt, bei der Mehrzahl in beiden Geschlechtern, bei den übrigen nur in dem einen. (Siehe Tabelle 1.)

Die Chromosomenzahl schwankt zwischen 11 und 32; 58 % der Arten haben 29—31 Chromosomen. (Siehe Diagramm II.)

Es ist auffallend, dass in fünf Familien eine Art mit einer stark verminderten Chromosomenzahl vorkommt. Die bedeutende Grösse dieser Chromosomen lässt auf Sammelchromosomen schliessen, die vermutlich infolge einer Mutation durch Fusion mehrerer Chromosomen entstanden sind. (Siehe Diagramm I.)

Bei vielen Arten ist die Chromosomenzahl in den beiden Geschlechtern verschieden. In dem einen Geschlecht sind zwei Chromosomen miteinander vereinigt, während sie in dem anderen frei sind. Die Fusion ist bei fünf Arten im weiblichen Geschlecht gefunden worden, im männlichen nur bei einer.

Auch verschiedene Rassen können verschiedene Chromosomenzahlen besitzen.

Die Chromosomenzahl der Spermatozyten eines und desselben Testis kann auch verschieden sein. Hier sind es vermutlich rein peristatische Einflüsse, die die Chromosomenzahl bestimmen.

Nur bei einer Art, *Augiades sylvanus*, konnte die zweite Reifeteilung im Ei erforscht werden. Hier kommt vermutlich ein Geschlechtschromosomenpaar vor, dessen Partner von verschiedener Grösse sind.

Die Chromosomenzahl ist ein phänotypisches Merkmal, das wie alle Eigenschaften teils von Genen, teils von der Umwelt bestimmt wird.

Bei der ontogenetischen Entwicklung spielt die Zahl der Chromosomen eine untergeordnete Rolle; die Gene der beiden Genome bestimmen die Entwicklung. Im Mechanismus der Keimzellenbildung, in erster Linie bei der Konjugation der maternellen und paternellen Chromosomen, ist dagegen die Chromosomenzahl von vitaler Bedeutung.

ERKLÄRUNG DER ABBILDUNGEN.

Sämtliche Photographien sind mit dem »Phoku» und dem Objektiv mit 120-maliger Eigenvergrösserung von ZEISS aufgenommen und sodann dreimal vergrössert. Alle Photographien sind unretuschiert.

Die Zeichnungen sind mit dem ABBE'schen Zeichenapparat auf Objekttischhöhe ausgeführt. Optik: ZEISS' apochromatisches Objektiv mit Eigenvergrösserung 120 und altes Kompensationsokular 12. Vergrösserung: ca. 2000 ×.

ZITIERTE LITERATUR.

1. BELIAJEFF, N. K. 1930. Die Chromosomenkomplexe und ihre Beziehung zur Phylogenie bei den Lepidopteren. — Z. f. ind. Abst.- und Vbgslehre, Vol. 54, S. 369—399.
2. CRETSCHMAR, M. 1928. Das Verhalten der Chromosome bei der Spermatogenese von *Orgyia thyellina* BTL. und *antiqua* L., sowie eines ihrer Bastarde. — Z. f. Zellforsch. und mikrosk. Anat., Vol. 7, pp. 290—399.
3. DARLINGTON, C. D. 1932. Recent Advances in Cytology. — London, Churchill.
4. DEDERER, PAULINE H. 1928. Variations in chromosome number in the spermatogenesis of *Philosamia cynthia*. — Journ. of Morph. and Physiol., Vol. 45, pp. 599—613.
5. DONCASTER, L. 1912. The Chromosomes in the Oogenesis and Spermatogenesis of *Pieris brassicæ*, and in the Oogenesis of *Abraxas grossulariata*. — Journ. of Genetics, Vol. 2, pp. 189—200.
6. FEDERLEY, H. 1929 a. Methoden zur Erforschung der Vererbung bei den Lepidopteren. — Handb. der biol. Arbeitsmethoden von E. ABDERHALDEN, Abt. 9, Teil 3, pp. 637—690.
7. — 1929 b. Über subletale und disharmonische Chromosomenkombinationen. — Hereditas, Vol. XII, pp. 271—293.
8. — 1932. Fortgesetzte Untersuchungen über die Subletalität gewisser Kombinationen von Geschlechtschromosomen. — Bulletins of the Laboratory of Genetics, No. 9, Leningrad, pp. 121—128.
9. — 1937. Fusion zweier Chromosomen als Folge einer Kreuzung. — Acta Soc. pro Fauna et Flora Fenn., Vol. 60, pp. 685—695.
10. FROLOWA, S. L. und ASTAUROW, B. L. 1929. Die Chromosomengarnitur als systematisches Merkmal. — Z. f. Zellforsch. und mikrosk. Anat., Vol. 10, pp. 201—213.
11. GOLDSCHMIDT, R. 1932. Untersuchungen zur Genetik der geographischen Variation. IV. Cytologisches. — Roux' Archiv für Entwicklungsmechanik der Organismen, Vol. 126, pp. 592—612.
12. GRÖNBLOM, TH. 1936. Verzeichnis der Gross-Schmetterlinge Finnlands mit Rücksicht auf ihre Verbreitung in den verschiedenen Provinzen. — Acta Soc. pro Fauna et Flora Fenn., Vol. 58, N:r 5, pp. 1—44.
13. HARRISON, J. W. H. and DONCASTER, L. 1914. On Hybrids between Moths of the Geometrid Sub-Family *Bistoninæ*, with an Account of the Behaviour of the Chromosomes in Gametogenesis in *Lycia* (*Biston*) *hirtaria*, *Ithysia* (*Nyssia*) *zonaria* and in their Hybrids. — Journ. of Genetics, Vol. 3, pp. 229—248.
14. HEILBORN, O. 1937 a. The Mechanics of so-called Secondary Association between Chromosomes. — Hereditas, Vol. XXII, pp. 167—188.
15. — 1937 b. Notes on Chromosome Associations. — Cytologia, FUJII Jubilee Vol., pp. 9—13.
16. HENKING, H. 1890. Untersuchungen über die ersten Entwicklungsvorgänge in den Eiern der Insekten. I. Das Ei von *Pieris brassicæ*. — Z. f. wiss. Zool., Vol. 49.
17. JOLLOS, V. 1931. Genetik und Evolutionsproblem. — Verhandl. der Deutschen Zoolog. Gesellschaft, 1931, pp. 252—295.

18. KAWAGUCHI, E. 1937. Chromosomenketten beim Rassenbastarde des Seidenspinners *Philosamia cynthia*. — Cytologia, FUJII Jubilee Vol., pp. 1023—1032.
19. KERNEWITZ, B. 1914. Über Spermiogenese bei Lepidopteren. — Zoolog. Anz., Vol. 45.
20. — 1915. Spermiogenese bei Lepidopteren mit besonderer Berücksichtigung der Chromosomen. — Arch. Nat.-Gesch., Abt. A., Vol. 81.
21. LESLEY, M. M. and FROST, H. B. 1927. Mendelian Inheritance of Chromosome Shape in *Matthiola*. — Genetics, Vol. 12, pp. 449—460.
22. LEVITSKY, G. A. 1930. Investigation on the Morphology of Chromosomes. — Proceedings of the U. S. S. R. Congress of Genetics, Plant- and Animal-Breeding in Leningrad 1929, pp. 87—105.
23. — 1931. The Morphology of Chromosomes. — Bulletin of Applied Botany, of Genetics and Plant-Breeding, Vol. 27, pp. 19—174.
24. MAKINO, S. 1935. Phylogenetic Relation of Lepidoptera and Trichoptera, reviewed from the Studies on their Chromosome-Complex (Collective review). — The Japanese Journ. of Genetics, Vol. 11, pp. 288—292.
25. MORGAN, L. V. 1922. Non-criss-cross inheritance in *Drosophila melanogaster*. — Biol. Bull., Vol. 42, pp. 267—274.
26. MUNSON, J. P. 1906. Spermatogenesis of the Butterfly, *Papilio rutulus*. — Proc. of the Boston Society of Nat. Hist., Vol. 33, pp. 43—124.
27. NAWASCHIN, M. 1925. Morphologische Kernstudien der *Crepis*-Arten in bezug auf die Artbildung. — Z. f. Zellf. und mikr. Anat., Vol. 2, pp. 98—111.
28. PCHAKADZE, G. M. 1930. Karyologische Untersuchungen an Trichopteren. — Arch. Russes d'Anatomie, d'Histologie et d'Embryologie, Vol. 9, pp. 227—321.
29. REGNART, H. C. 1930. Additions to our Knowledge of Chromosome Numbers in the Lepidoptera. — Proc. of the University of Durham Philosoph. Soc., Vol. 9, pp. 79—83.
30. SEILER, J. 1914. Das Verhalten der Geschlechtschromosomen bei Lepidopteren. — Arch. f. Zellforsch., Vol. 13, pp. 159—269.
31. — 1922. Geschlechtschromosomen-Untersuchungen an Psychiden. III. Chromosomenkoppelungen bei *Solenobia pineti* Z. — Ibid. Vol. 16, pp. 171—216.
32. — 1925. Zytologische Vererbungsstudien an Schmetterlingen. I. Ergebnisse aus Kreuzungen von Schmetterlingsrassen mit verschiedener Chromosomenzahl. Ein Beweis für das Mendeln der Chromosomen. — Arch. JULIUS KLAUS-Stiftung für Vererbungsforschung, Sozialanthropologie und Rassenhygiene, Vol. I, pp. 63—117.
33. SEILER, J. und HANIEL, C. B. 1921. Das verschiedene Verhalten der Chromosomen in Eireifung und Samenreifung von *Lymantria monacha* L. — Z. f. ind. Abst.- und Vbgslehre, Vol. 27, pp. 81—103.
34. STEVENS, N. M. 1906. Studies in Spermatogenesis. II. A comparative study of the heterochromosomes in certain species of Coleoptera, Hemiptera and Lepidoptera, with especial reference to sex-determination. — Carnegie Institution of Washington, Public. No. 36, Part II, pp. 33—74.
35. SVESHNIKOVA, I. N. 1927. Karyological Studies in *Vicia*. — Bull. of Applied Botany, of Genetics and Plant-Breeding, Vol. 17, pp. 37—72.
36. YATSU, N. 1913. Notes on the Spermatogenesis of the wild and the domesticated Silkworms. — Annot. Zoolog. Japon., Vol. 8.

INHERITED SEX-MOSAIC IN MAN AND THE STATISTICAL TREATMENT OF SUCH DATA

AN ANSWER TO PROFESSOR S. G. LEVIT

BY *GERT BONNIER*

INSTITUTE OF ANIMAL BREEDING, WIAD, ELDTOMTA, SWEDEN

IN a study of inherited sex-mosaic in Man (PETTERSSON and BONNIER, 1937) a case found by PETTERSSON was described, a review was made of similar cases, described in the current literature, and an attempt was also made at a genetical analysis. While this paper was being printed Dr. O. TEDIN, who had read the manuscript, called attention to an error in the statistical method employed in the analysis of the data. The issue of Hereditas, in which the study was to be printed, was at that time nearly ready for distribution, and the addition of a correcting amendment would have caused considerable trouble. As the error — although deplorable and unnecessary — did not influence the main conclusion we decided to let the matter rest until somebody should eventually criticize the method employed. Such criticism has now been published (LEVIT, 1937), and the author will avail himself of the opportunity to point out the consequences of the error in regard to the genetical problem involved, and to answer such parts of the criticism which he is unable to accept.

In the criticized paper it was pointed out that BONNIER alone was responsible for the review of the literature and for the genetical analysis. This answer is, therefore, by BONNIER alone.

In the study in question similar cases of intersexuality were brought together from 5 different families. Individuals who in all apparent characters were of the female sex, and who were generally considered to be women — some of them had even married — were found to be lacking vagina and uterus, but had more or less well developed testicles. (For all details see PETTERSSON and BONNIER, 1937). These cases of intersexuality were considered to be of a hereditary nature, since all the 5 families were chosen because at least 2 cases were known within each family. The main conclusion drawn from the numerical proportions within the material was that the intersexes are genetical males, i. e. their

chromosomal constitution is *XY*. It seemed most probable that the mosaics were the result of a sex-linked recessive gene, but it was also possible that the gene in question was autosomal and semi-dominant. In consequence, within all groups of brothers and sisters where segregation occurs, the relation between normal men and intersexes should be 1 : 1. If the data were pooled from all groups of brothers and sisters within which the abnormality had occurred or where some individual was shown by its progeny to carry the gene in question, there were 22 ♀ : 8 ♂, and this proportion was considered as significantly different from 1 : 1, when the data were fitted to the complete binomial distribution. The obvious error is that since families with 0 or 1 abnormal individuals were excluded by the method of collecting the data, the complete binomial distribution should not be used in calculating the expected proportions. LEVIT has pointed out this error, and he considers the proportion 22 : 8 to be in good correspondence with the numbers expected upon the hypothesis.

In order to explain the proportion 22 : 8, which we considered to be significantly different from 1 : 1, different auxiliary hypotheses were suggested. It was, however, also pointed out that such additional hypotheses are rather a nuisance. The consequence of LEVIT's criticism is that these auxiliary hypotheses are unnecessary, and the main conclusion — that the intersexes are genetical males — is the more satisfactorily proved. In LEVIT's paper this fact is not pointed out, and it is possible that readers who give a cursory glance to our paper and LEVIT's criticism might form the opinion that our conclusions were completely erroneous. This would be deplorable, as the great probability that a certain comparatively common type of human intersexes is genetically male is directly opposed to generally accepted theories. It is not only GOLDSCHMIDT (e. g. GOLDSCHMIDT, 1931) who considers all human intersexes to be genetically female, but his opinion is repeated in monographs and text-books (e. g. BERNER, 1930 and MOHR, 1935).

LEVIT considers it incorrect to use, in the statistical treatment, only such families where there are at least two abnormal individuals, especially »since it is perhaps true that when there is a large number of affected individuals the case is more likely to be given space in the literature». When looking through the literature in connection with our study of the actual case, I found a large number of cases, where only one intersex of the type studied was described. (No notes were made about those cases and as I have no time to go through the extensive literature once more I cannot give any definite numbers.) If

cases with more than one intersex in the family are more liable than single cases to be quoted in the literature, the large number of the latter indicates that many of them are not of a hereditary nature. It seems to be correct, therefore, in cases like the present and similar ones, when the heredity of a certain pathological character is studied, to use only families with at least two affected individuals. But obviously correct statistical methods must be used.

The analysis made by LEVIT is based upon the standard deviation of incomplete binomial series, and he uses formulae for the variances, calculated by BERNSTEIN (1929 and 1932). It may be pointed out, however, that since the binomial series are discontinuous and unsymmetrical, this method may yield erroneous results. In order to obtain the true distributions and the correct value of the probability, P, the following method must be used. If the probability for the occurrence of the abnormality is p and $q = 1 - p$, and if we have n groups of brothers and sisters with S_1, S_2, . . . S_n individuals of the actual kinds (♀ and ♂ in our case), the true distribution is obtained by the formula

$$(p + q)^{S_1}(p + q)^{S_2} \ldots (p + q)^{S_n}.$$

In developing each factor those terms are excluded which correspond to such numbers of abnormal individuals as cannot occur with the methods used in selecting the material. After multiplication all terms are added which deviate as much or more from the mean of the series as the total number of abnormal individuals found, and this sum is divided by the total of the series. (The mean may be obtained directly, and the total from the formula after multiplication, by exchanging each factor by 1 less the sum of the excluded terms.) The quotient obtained is the correct value of probability, P. In our case the 5 families had 12 groups of brothers-sisters, as follows:

S	2	3	6	2	2	2	2	2	3	2	3	1
Lowest number of affected individuals	2	2	2	1	1	1	1	1	0	1	1	1

In developing each of the three first factors the first two terms are excluded; from the five following, the first term; in the next factor no term, and in the three last ones, the first term. In our case $p = q$, and the calculations may be simplified by using $p = q = 1$. The true distribution is then found to be:

Number affected	14	15	16	17	18	19
Expected frequency.....	8640	74880	304080	770256	1365860	1801968
Number affected	20	21	22	23	24	25
Expected frequency.....	1832763	1467449	935070	475599	192273	61056
Number affected	26	27	28	29	30	Total
Expected frequency.....	14907	2701	342	27	1	9307872

The mean value is 19,725, the observed number was 22, and all values except 18, 19, 20 and 21 are as far from the mean as 22, or farther. The sum of these frequencies, divided by the total, is 0,3051, and this is the true value of P. It is obvious that LEVIT's opinion is correct, that there is a very good correspondence between the expected and the actual value.

The difference between the mean and the number observed is $22 - 19{,}725 = 2{,}275$. The standard deviation of this mean is obtained by calculating the variance of each of the factors $(p + q)^S$ after excluding the proper terms, and taking the square root of the sum of variances. The variances of the individual factors may be calculated from the developed series or by aid of the formula of BERNSTEIN, used by LEVIT. In this case the difference is of no importance, but in cases where the value of P approaches the level of significance it may be of great importance to use the correct binomial method instead of standard deviations and the normal distribution.

The difference between the two methods is illustrated by the following example. We assume a number of brother-sister groups, each

Number of brother-sister groups of 4	Mean value	Standard deviation	Number affected	Exact value of P	Value of P based on the normal distribution
1.....	2,545454	0,655555	4	0,090909	0,026501
2.....	5,090909	0,927094	7	0,074380	0,039476
3.....	7,636363	1,135460	10	0,059354	0,037371
4.....	10,181818	1,311109	13	0,046513	0,031595
5.....	12,727272	1,465865	16	0,036330	0,025577
10.....	25,454545	2,073046	30	0,033151	0,028338

with 4 individuals; further, that these are so chosen that at least two individuals are affected, and, finally, that $p = q = {}^1/_2$. In the table above some values are given for material consisting of 1, 2, 3, 4, 5, and 10 such families, and in each case the assumed number of affected individuals is chosen in such a way that the true value of P shall be as close to 0,05 as possible. In all cases this true value of P is higher than the one obtained if the standard deviation and the normal distribution are used, although the difference decreases with an increasing number of families. In human genetics, however, the material is often limited to a small number of families.

SUMMARY.

1. In a previous paper (PETTERSSON and BONNIER, 1937) it was shown that a certain type of human intersexes, who had testicles but a female exterior, and who were generally considered to be women (some had even married), most probably were genetical men, i. e. they had the chromosomal constitution *XY*.

2. According to this hypothesis the intersexes and normal men should occur in the proportion 1 : 1, whereas the number found were 22 : 8. This deviation was considered to be significant, and some alternative auxiliary hypotheses were suggested. It was pointed out, however, that the need of such hypotheses rather tends to weaken the proof of the main one.

3. In a criticism of our paper, LEVIT (1937) has called attention to the fact that the proportion 22 : 8 is in good accordance with the expected value 1 : 1; the opposite opinion was the result of a mistake in the statistical treatment of the data. The consequence is that no auxiliary hypotheses are necessary, and that the main hypothesis — the *XY* nature of the intersexes — must be considered to have been proved still better than in our first presentation of the data.

4. There are numerous cases described in the literature, where an isolated intersex of the type dealt with has occurred. It is rather probable that several of these cases are of non-hereditary nature. It seems necessary, therefore, to exclude all families unless at least two cases of intersexuality are known. The opposite opinion of LEVIT cannot be accepted.

5. LEVIT carries out an analysis of the data using the standard deviations and the normal distribution. It is shown in this paper that when the samples are small, as is often the case with human material,

the use of the standard deviation may lead to erroneous results. The method used by LEVIT cannot, therefore, be recommended, and it is necessary to calculate the exact binomial distributions in each case.

LITERATURE CITED.

1. BERNER, O. 1930. Hermaphroditismus und Geschlechtsumwandlung. — Handbuch innere Sekretion 2.
2. BERNSTEIN, F. 1929. Variations- und Erblichkeitsstatistik. — Handb. Vererbungsw.
3. — 1932. Korrekturen bei erblichkeitsmathematischer Untersuchung von Krankheiten mit rezessivem Erbgang. — Arch. Rass. Ges. 27.
4. GOLDSCHMIDT, R. 1931. Die sexuellen Zwischenstufen. — Berlin.
5. LEVIT, S. G. 1937. Genetical analysis of selected human data bearing on the genetics of hermaphroditism. — Journ. of Genet. 35: 151—159.
6. MOHR, O. L. 1935. Arvelighet og sykdom. — Oslo.
7. PETTERSSON, G. and BONNIER, G. 1937. Inherited sex-mosaic in Man. — Hereditas XXIII: 49—69.

THE EFFECT OF COLCHICINE ON ROOT MITOSES IN ALLIUM

BY *ALBERT LEVAN*
HILLESHÖG, LANDSKRONA, SWEDEN

AFTER BLAKESLEE and AVERY (1937) had made the sensational discovery of the induction of chromosome doubling by colchicine treatment it became a question of prime importance to investigate the cytological mechanism causing this doubling. It has long been known that colchicine acts disturbingly on the normal course of mitosis (DIXON, 1905). DUSTIN (1934) and LITS (1934) regarded colchicine as a very active agent for increasing the number of mitoses in a tissue (a »poison caryoclasique»). LUDFORD (1936), however, came to the conclusion that the increase in the number of the mitoses after colchicine treatment was due to an »accumulation of arrested mitoses» rather than to a stimulation process. He attributed this effect to a »failure of the mitotic spindle to form and function in the normal manner». NEBEL and RUTTLE (1938), who first studied the effect of colchicine on plant cells (stamen hairs of *Tradescantia*), arrived at a similar result.

The material of the experiments dealt with in the present paper consists of root tips of *Allium fistulosum* and *Cepa*. Root tips of *A. fistulosum* were secured from bulbils that had overwintered in the field, while in the case of *A. Cepa* large bulbs were used. The *fistulosum* form used had a hybrid chromosome garniture, consisting of somatically 15 medially attached chromosomes and 1 typical *fistulosum* s_1 (LEVAN, 1936, Fig. 1 *b*). The *Cepa* form had the chromosomes characteristic of this species, *viz.* 14 medially and 2 subterminally attached chromosomes (LEVAN, l. c., Fig. 1 *a*).

The experiments were arranged in the following way. Bulbs with rapidly growing root tips, 0,5—1,0 cm in length, were immersed for exposure into colchicine solutions during periods of different length. Root tips were then fixed at certain intervals after the transfer of the bulbs from the colchicine solutions into pure water. The fixations were made in NAVASHIN under air evacuation. The material was embedded and cut into transverse and longitudinal sections, the former being 20 μ in thickness, the latter 20—30 μ. The slides were stained in gentian violet, some also in »lichtgrün».

I. DESCRIPTION OF THE TYPICAL COURSE OF THE C-MITOSIS.

In the first series of experiments the conditions were the following:

Concentrations of colchicine: 0,125, 0,25, 0,5, 1,0, 2,0 %.

Exposure times: 7, 15, 30 min., 1, 2, 24, 72 hours.

Fixing took place: 0, 15, 30 min., 1, 3, 6, 12, 24, 48, 72 hours after finishing the colchicine treatment.

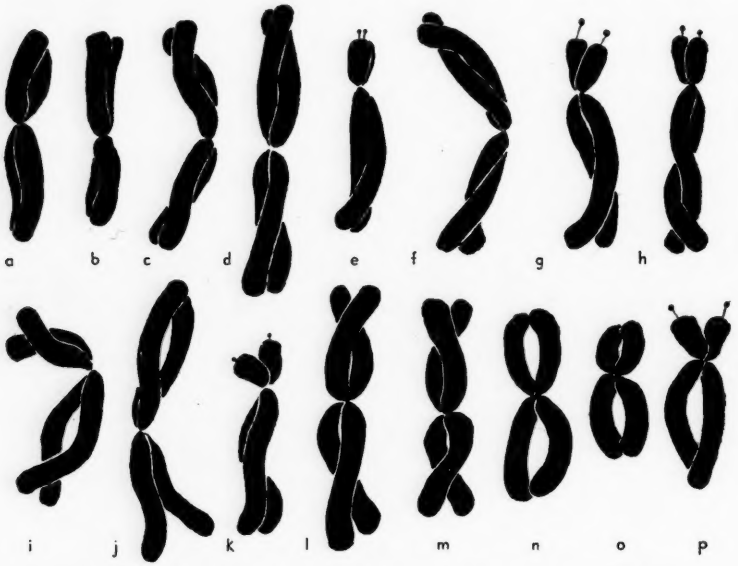


Fig. 1. The first stages in the development of the c-pairs. — × 3900.

The effect of colchicine on the course of mitosis is entirely specific, and the modification in mitotic behaviour will be abbreviated »c-mitosis». The c-mitosis can be referred to one single moment, *viz.* an inactivation of the spindle apparatus connected with a delay of the division of the centromere. The effect thus produced may be expressed as a completion of the chromosome mitosis without nuclear or cellular mitosis.

The prophase stages take place normally: the chromosomes divide, condense, and assume metaphase appearance. They are, however, not arranged into an equatorial plate. Instead they are all the time scattered over the cell in a diakinesis-like manner. This condition lasts

for a long time after the disappearance of the nuclear membrane. The halves of each chromosome are seen to be coiled around each other in a relational spiral (Fig. 1 *a—h*). This spiral is then slowly uncoiled, and during this process the chromosomes assume a whole series of shapes exceedingly characteristic of the c-mitosis and never occurring normally. At first loops are formed between the undivided centromeres and the points where, on account of the spiralisation tension, the chromatids touch each other. There usually occurs one such point on each of the long chromosome arms (Fig. 1 *i—p*). These points of contact move slowly towards the ends, and at last the chromatids touch each other only at the still undivided centromere and at one or both ends

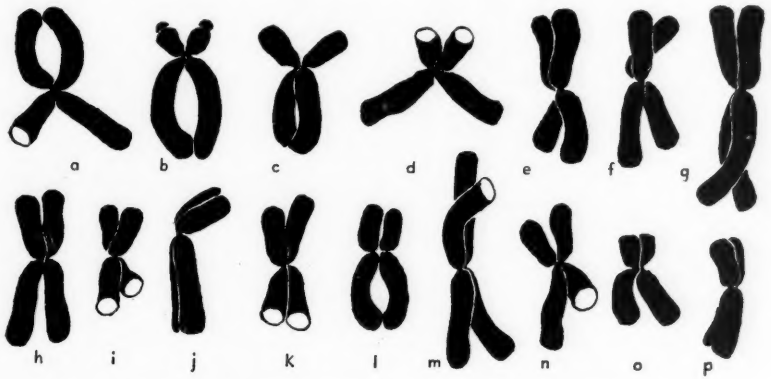


Fig. 2. *Allium fistulosum*, the 16 c-pairs of one cell separately drawn. — × 3900.

(Fig. 1 *n*, *o*; Fig. 2 *a*, *l*). This process strikingly resembles the terminalisation of chiasmata in diakinesis bivalents. At last the ends also slip off, and the half-chromosomes are now held together only at the undivided centromeres. Instances of such typical cross-shaped pairs (called below c-pairs) are reproduced in Figs. 2 *d*, *n* and 3 *b—d*.

As has already been mentioned, the formation of the c-pairs is peculiar to material treated with colchicine. Their origin is evidently due to the delay of the division of the centromere. In the course of normal mitoses the centromere divides at about the same time as the chromosomes are arranged into the equatorial plate, and the orientation towards the poles is probably simply conditioned by the division of the centromeres (»auto-orientation», DARLINGTON, 1937). Anyhow, the later stages in the uncoiling of the relational spiral normally occur within the

equatorial plate. After that the centromeres separate and proceed towards the poles, pulling the chromosome arms behind.

The c-pairs form the configuration most commonly found the first few hours after the colchicine treatment. This indicates that the division of the centromere is delayed for quite a considerable time. This is, partly at least, the cause of the apparent impression of mitotic stimulation, which is always found after c-treatment. The prophases arrive at metaphase and are kept at that stage for a long period until the centromere finally divides.

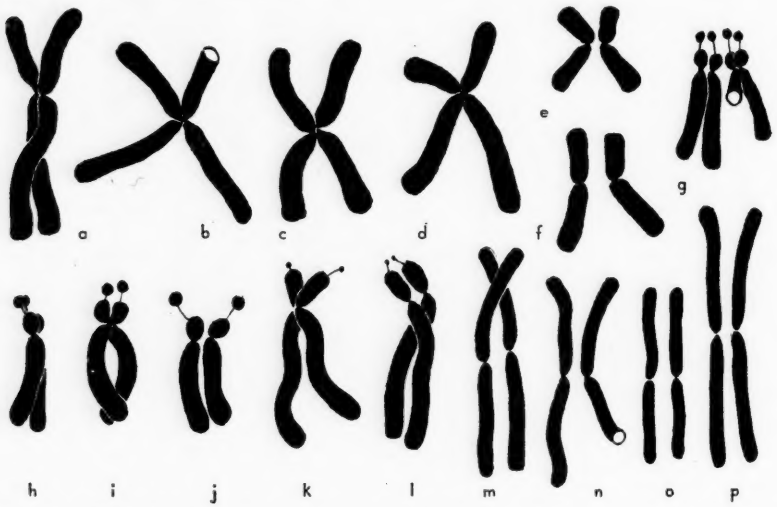


Fig. 3. The division of the centromere within the c-pairs. *A. Cepa: a—b, k—l; fistulosum: c—j, m—p.* — × 3500.

During this period no normal anaphases are found in the slides. If certain cells are at anaphase at the onset of colchicine action, they may form two telophase nuclei, if the anaphase is advanced far enough, and in certain cases a cell wall has been seen formed between the nuclei, but in most cases the anaphase chromosomes remain in 2 groups, which will later be included into one nucleus.

After a few hours the division of the centromeres finally takes place (Fig. 3 *e—l*), and the two daughter chromosomes are straightened out and locate themselves parallelly like »pairs of skis» (NEBEL and RUTTLE, l. c.). The centromeres are placed opposite one another in each pair (Fig. 3 *m—p*). The arrangement in pairs is often maintained also

through the following mitoses and is especially easy to observe in the case of s_1 chromosomes (Fig. 3 *g*). Incidentally this relative stability in the chromosome arrangement through several subsequent c-mitoses is very conspicuous and results in an accumulation of the same chromosome in one section of the nucleus. An instance of this is shown in Fig. 4 *a*, where at least 8 s_1 chromosomes are gathered at the same place.

It is often noticed during the c-anaphase that the division of the centromeres does not take place quite simultaneously within one cell. In Fig. 3, for instance, the still undivided pairs *c* and *d* are drawn from the same cell as the two divided ones, *e* and *f*. The division of the centromere has evidently been desyncronised as well as delayed. Now

Exposure	0 min.	15 min.	30 min.	1 hour	12 hours	24 hours	36 hours	48 hours
7 min.			A		B		C	
15 »			A		B		C	
30 »		A			B		C	
1 hour		A			B		C	
2 hours	A					B		C
24 »	A					B		C
72 »	A					B		C

Diagram 1. *The rhythm of the c-mitoses.*

A = the c-pairs appear. B = first indications of the spindle regeneration. C = normal spindle.

the chromosomes pass on into telophase and all of them are included in one nucleus, which will consequently contain the double somatic chromosome number.

After the short exposures, 7 min.—1 hour, there usually occurs only one c-mitosis, but after long exposures several c-mitoses may follow each other in the same cell, and each of them doubles the chromosome number.

The inactivation of the spindle apparatus under the influence of colchicine is reversible; after a period of 12—24 hours in pure water the spindle begins to regenerate. The regeneration takes place very characteristically and in the course of the transition to normal spindle all kinds of abnormities are seen: multipolar spindles, asymmetrically

or not at all compact spindles, etc. After 36—48 hours the mitoses again run their normal course.

In Diagr. 1 is given a survey of the rhythm of the c-mitoses, calculated from the experiments now dealt with. From this diagram is seen that after short exposures an interval of 30 minutes passes before the typical c-mitoses appear. This interval is necessary for the full development of the c-pairs, while the inactivation of the spindle probably occurs much earlier. Diagr. 1 also indicates that long exposures require a somewhat longer time for recovery than short ones.

II. CYTOLOGICAL CONSEQUENCES OF C-MITOSES.

About 48 hours after the c-exposure was finished, the mitoses have reassumed their normal course and persistent changes in the root cells produced by the colchicine treatment can be observed. After the short exposures (7—30 min.) such changes are rarely met with, nevertheless a few cells with 4x chromosomes may be found. The majority of cells show the normal diploid number. After an exposure of 1—2 hours a great percentage of 4x cells are found together with occasional 8x cells, and after the longest exposures (72 hours) cells with still greater chromosome numbers are seen, 32x being the upper limit in these series.

In order to get an idea of the distribution of different chromosome numbers in the roots after different c-exposures, I examined the cross-sections of the whole meristematic region of a few roots and plotted on diagrams all the chromosome numbers which could be determined. Determination of greater chromosome numbers than 8x could not always be made exactly, yet there was no difficulty in deciding whether a chromosome plate should be classified as 8x, 16x or 32x. The numbers were not strictly euploid, which is easy to understand in view of the frequently occurring anaphase disturbances. The plate reproduced in Fig. 4 *d* shows, for instance, 135 chromosomes, and though this number may not be exact it is certainly greater than 128, which corresponds to 16x.

The root diagrams were grouped into 5 or 6 regions from each root and the chromosome numbers from these regions were tabulated in Table 1, the treatment of the roots being specified in Table 2. A study of Table 1 will at once reveal one very important fact: there is a decided correlation between the chromosome number of a cell and the location of the cell in the root. A greater percentage of changed cells occurs in older parts of the root, while close to the root

TABLE 1. *The distribution of normal and changed chromosome numbers in 7 root tips.*

Region	Slide 4693			Slide 4694					Slide 4695				Slide 4696		
	2x	3x	4x	2x	3x	4x	6x	8x	2x	3x	4x	8x	2x	3x	4x
1	21	—	2	30	2	14	—	—	6	—	14	—	33	—	—
2	23	—	2	18	1	49	—	—	7	—	25	—	47	—	2
3	32	5	9	7	—	36	—	—	5	—	38	2	40	—	6
4	16	—	11	2	—	35	1	1	3	3	19	1	32	—	13
5	7	—	5	2	—	5	1	—	—	—	1	—	19	2	19
6	—	—	—	—	—	—	—	—	—	—	—	—	12	—	22
Total	94	5	29	59	3	139	2	1	21	3	97	3	183	2	62

Region	Slide 4739					Slide 4741				Slide 4912			
	2x	4x	8x	16x	32x	2x	4x	8x	16x	2x	4x	8x	16x
1	5	16	—	—	—	8	16	—	—	17	—	—	—
2	5	19	7	—	—	3	39	5	—	12	9	—	—
3	—	12	8	—	—	—	27	19	—	13	15	1	—
4	—	2	12	3	—	—	11	15	—	10	18	1	—
5	—	—	3	1	1	—	2	2	2	3	7	3	1
6	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	10	49	30	4	1	11	95	41	2	55	49	5	1

TABLE 2. *Particulars about the roots of Table 1.*

Slide	Number of sections in each region	The treatment of the roots		
		% colchicine	exposure time	fixing time
4693	10	0,125	2 hours	72 hours
4694	10	0,250	»	»
4695	10	0,5	»	»
4696	10	1,0	»	»
4739	5	0,5	72 hours	48 hours
4741	8	2,0	»	»
4912	7	0,01	144 hours	72 hours

tip among the new meristematic cells normal diploid numbers prevail. This situation is made clear in Diagr. 2, where the percentages of diploid cells in different regions of 4 roots are graphically represented. In all of the root tips this percentage increases towards the tip of the root.

The absolute values are, it is true, highly different in different roots, and they are evidently due to fairly arbitrary conditions. However, they afford a measure of the susceptibility of the meristematic cells to colchicine action in the course of the exposure.

The situation just described seems to be generally valid throughout the colchicine experiments of the present study. It is of fundamental significance. If for some reason there occurs a population of cells with different chromosome numbers within an embryonic tissue, a selection

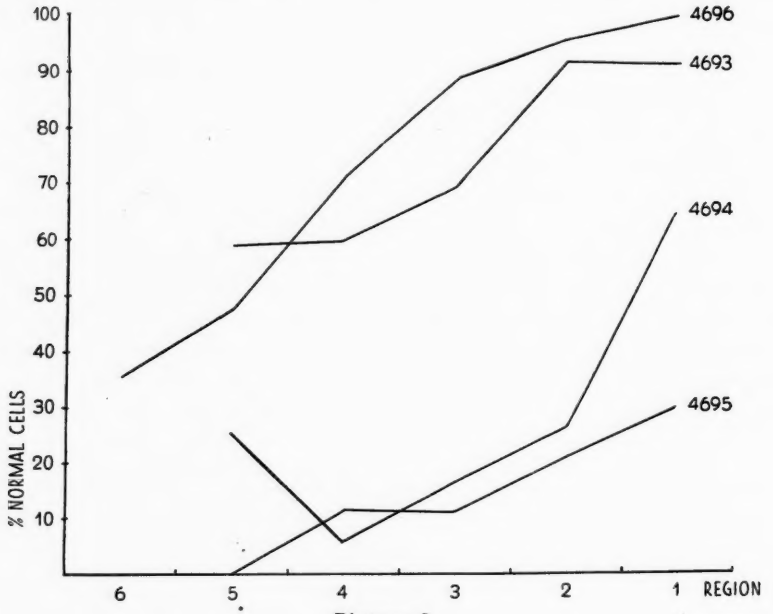


Diagram 2.

among the cells immediately sets in. Normal 2x cells are favoured at the expense of cells changed by colchicine. The primary cause of this is probably the division rate, which seems to be more rapid in diploid than in polyploid cells. Moreover, normal unchanged cells start their first division after the c-treatment more readily than do changed cells. At a certain moment after the transfer from the colchicine solution, frequent diploid mitoses are seen, while highly polyploid giant nuclei still linger in prophase stages.

As regards the roots recorded in Table 1, the diploid cells have in

no case totally disappeared. Even after an exposure of 72 hours there occur numerous diploid cells in the sections close to the tip. When colchicine is used for the production of polyploid forms, this fact must be kept in mind. Throughout a considerably prolongated colchicine treatment single cells of the meristeme can keep themselves in a condition resistant to colchicine. After the conclusion of the treatment these cells may constitute a very trifling minority, but thanks to their favoured situation in the competition with polyploid cells they will predominate again after some time. The tissue thus shows a tendency to return to its original cytological state.

III. THE REITERATION OF THE C-MITOSES.

The preceding chapter leads to the question: How far can the cells be changed by colchicine, where is the limit of the capability of the cell to respond to an extremely prolongated c-exposure with new c-mitoses? Even the strongest dose of colchicine used in the above experiments (2 % colchicine for 72 hours) did not entirely kill the cells. After their transfer into water the cells might revert again to the normal mitosis. Judging from the chromosome numbers then observed there had taken place at least 4 generations of c-mitoses in the course of the exposure. The number 128 frequently occurred in the cells and in one case ± 256 chromosomes could be counted with certainty. It is clear, however, that in this experiment the lethality limit cannot have been far off.

In order to investigate if a longer exposure in a weaker colchicine solution might give a still more extreme final result, the following two experimental series were arranged. 5 bulbs were placed in 0,01 % colchicine and 5 in 0,1 %. They were transferred daily into new-prepared colchicine solutions in order to diminish the risk of putrefaction. 6, 8, 10, 12, and 14 days after the beginning of the exposure one bulb from each series was transferred into pure water, and root tips were fixed several times from each bulb.

A poisoning effect of colchicine could actually be observed in these experiments. The bulbs immersed in 0,1 % solution manifested a much slower growth of the leaf shoots than the bulbs in 0,01 %. On the seventh day the former showed leaf shoots about 8 cm in length, the latter on an average 15 cm, while an untreated control bulb had shoots 34 cm in length.

In many of these bulbs the limit of cell lethality had been passed. C-mitoses were, it is true, going on in most of them at the first fixation

time, but as a rule they were incapable of reverting into normal mitoses. In these roots enormously high chromosome numbers were found. In some cases the numbers could be fairly correctly estimated, and numbers as high as 500 and 1000 c-pairs were not rare. In c-mitoses, how-

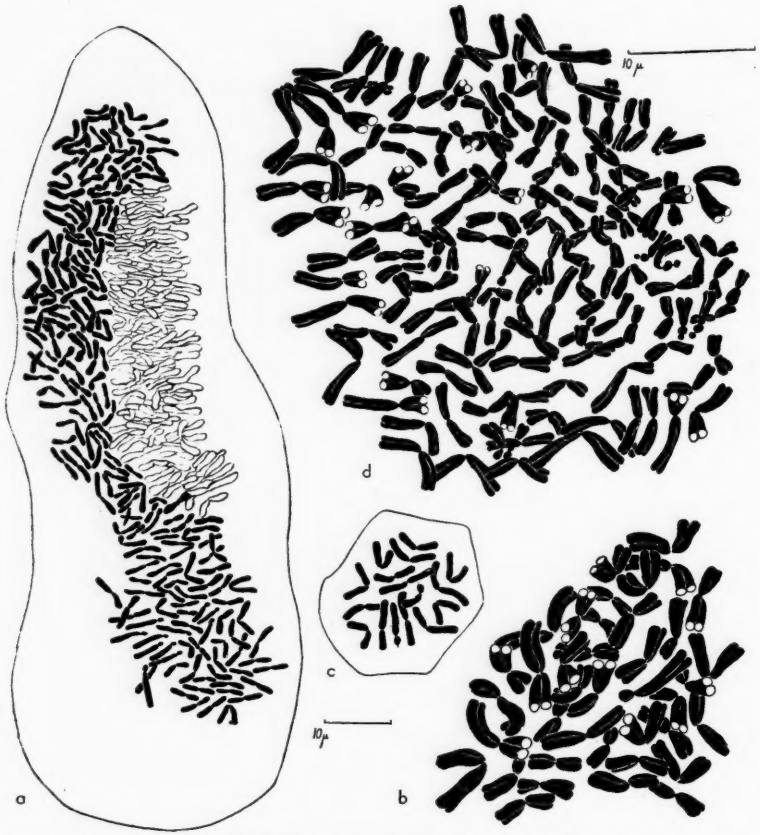


Fig. 4. Normal mitoses after the regeneration of the spindle. *A. Cepa*: *a—c, fistulosum*: *d*; *a*: ± 500 chromosomes, *b*: 16 chromosomes, *c*: detail of *a*, *d*: ± 135 chromosomes. — *a, c* × 1000, *b, d* × 2000.

ever, the chromosomes are equally scattered out spherically and so their number is extremely difficult to determine. Judging from the size of the cells and the chromosome clusters, there occurred still higher numbers than 1000 pairs. At least 6 c-mitoses, probably more, have taken

place here. The fixations were excellent and the c-pairs could be closely studied. They showed the same characteristic features as are described in Chapter I.

In some slides fixed 24—48 hours after the exposure was finished, normal divisions could be studied. In these slides the chromosomes were arranged in equatorial plates and their numbers could be determined with a fairly high degree of certainty. About 500 chromosomes constituted the upper limit so far met with in these slides; thus, greater numbers seem to be unable to revert into normal mitosis.

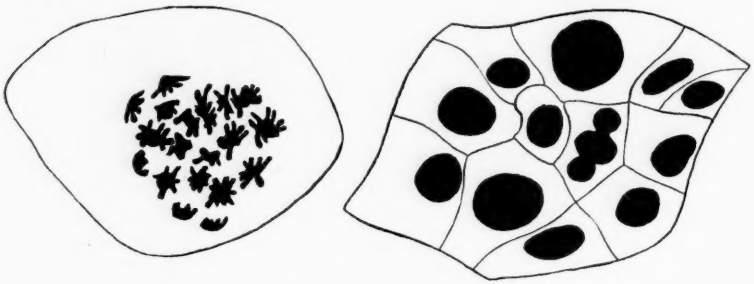
The problems of cell mechanics which are elucidated in connection with the origin of these fantastically great chromosome numbers will only be touched upon on this occasion. The cells have considerably increased in volume. The macroscopically observable tumours (Figs. 6 and 7; BLAKESLEE and AVERY, l. c., Fig. 4 B^1) are simply caused by this enormous increase in cell volume. *The same cells which at the beginning contained 16 chromosomes have been adapted to house 500 or 1000 chromosomes.* The increase in volume is, however, not sufficient to allow the mitoses with the new great chromosome numbers to take place without being severely disturbed by crowding. Divisions with 64 chromosomes still go on quite regularly, but plates with 128 chromosomes and more are often bent and twisted on account of lack of space. Often the centre of a plate forms a cupola and is found in one section while the ring-shaped periphery lies in the neighbouring section. Part of one plate may bend into a level at right angles with the rest of the plate or turn round 180°, etc. The plate reproduced in Fig. 4 *a* probably contains about 500 chromosomes. As is seen from the detail drawing Fig. 4 *c*, the appearance of the chromosomes is quite normal, although they are more crowded than normally. Fig. 4 *a* is drawn under low magnification from 2 sections and is not intended to give the exact number and shape of the chromosomes, but only a survey of the whole cell.

The chromosomes are especially over-crowded in the embryonic vascular tissue, the cells of which are extended in length. In such cells it happens that after reiterated c-mitoses the nucleus completely fills the cell. The nucleus thus gets lengthened and spool-shaped. Normal mitosis can take place, however, also under such conditions. The equatorial plate then resembles the corresponding stages in the pollen tube mitosis.

The transition from c-mitosis to normal mitosis in these cells with high chromosome numbers has a very characteristic course. The first

indication of spindle regeneration is that the telophase chromosomes are not included into a rounded nucleus. Instead they gather together into an often large number of small groups, which are never completely separated from each other. The nucleus thus formed gets a highly irregular shape and is perforated by numerous holes and canals.

The next step in the spindle recovery is indicated by the plainly multipolar spindle. This results in the gathering of the chromosomes into some 20 clusters, which are wholly separated from each other (Fig. 5 *a*), and at telophase they form as many small nuclei. Between these nuclei there are often formed real cell walls, stained green by »lichtgrün» (Fig. 5 *b*). By this peculiar mechanism a giant cell is divided into a large number of minor cells, which of course obtain varying sets of chromosomes and will mostly be non-viable. A point



a *b*

Fig. 5. The transition to normal mitosis, *a*: multipolar telophase, *b*: a giant cell has been divided into many minor cells. — × 750.

of considerable interest which may be noted is that as a consequence of a spindle abnormality one way has been opened for the reduction of the chromosome number in somatic cells. This mechanism, however, acts very irregularly and is of quite a different nature from the case of somatic reduction described by STEIN (1936).

When the multipolar divisions have been going on for some time the number of poles is gradually reduced and at last all cells have regained normal bipolar spindles.

The different stages in spindle recovery are continuously intermingled, but the different types described above are sufficiently clear to be identified in longitudinal sections as 3 regions: in the upper region of the root the lobed giant cells are found, then follows the region with giant cells divided into small cells, and at the root tip normal bipolar mitoses predominate.

IV. THE LOWER THRESHOLD VALUE OF COLCHICINE ACTION.

In order to determine the lowest concentration necessary for the induction of c-mitoses, two series of experiments were performed. The first of them included the following concentrations: 0,0001, 0,0005, 0,001, 0,005, 0,01, 0,05, 0,1 %. The roots were exposed in these solutions for 4 hours, and were then fixed 0, 8, 24, and 48 hours after the transfer to pure water.

The lowest concentrations (0,0001—0,005 %) did not produce c-mitosis, while from 0,01 % and upwards the c-mitoses were conspicuous. Also on the second occasion of fixing (after 8 hours) the c-mitoses were taking place in all the concentrations except 0,01 %, where the new meristematic cells showed normal mitosis. In older parts of the 0,01 % roots, however, the colchicine-induced disturbances earlier observed could be traced. The recovery of the spindle is evidently more rapid after exposures in low concentrations. At first, however, the c-mitoses were as conspicuous in 0,01 % as in the stronger solutions.

The second experimental series was intended especially to elucidate the threshold region limited by the former series to 0,005—0,01 %. It contained the following 11 concentrations: 0,0050, 0,0055, 0,0060, 0,0065, 0,0070, 0,0075, 0,0080, 0,0085, 0,0090, 0,0095, 0,0100 %. Also this time the exposures were made for 4 hours and fixing was made after 0, 8 and 24 hours. The same variety of *A. Cepa* was used in both series.

Even the concentration 0,0055 caused disturbances of the spindle function. Of great interest is the observation of a fractionating of the disturbances. In treatment with increasing concentrations the exterior spindle is first damaged (in 0,0055 %), while the centromeres are normally divided still in a concentration of 0,0070 %. Above this concentration the first traces of c-pair formation appear. The c-pairs are, however, not of the characteristic appearance until a concentration close to 0,01 % is reached. After 8 hours all new mitoses were normal throughout the whole series, and the spindle apparatus had completely recovered. In this connection reference should be made to the observations of DARLINGTON and THOMAS (1937) as to the individuality of the two co-operating factors of normal spindle function, the exterior or centrosomic factor and the interior or centromeric factor.

The threshold value of root mitoses of *A. Cepa* has thus been fixed to an exposure of 4 hours in 0,005—0,01 % colchicine solution. As a comparison it may be mentioned that NEBEL and RUTTLE (l. c.) found the

threshold value of *Tradescantia* to be just above 0,004 %. LUDFORD (l. c.), working with animal material, found a very much higher susceptibility to colchicine: the action arresting mitosis could be observed as far down as in a 0,00001 % solution.

V. THE PRACTICAL SIGNIFICANCE OF COLCHICINE.

Although the studies on the action of colchicine dealt with on the present occasion are of a preliminary nature, based as they are on only 1 month of experimenting, they nevertheless furnish, in the writer's

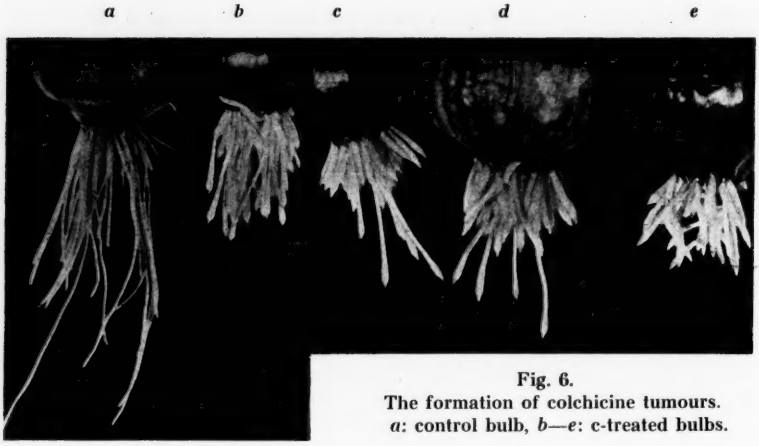


Fig. 6.
The formation of colchicine tumours.
a: control bulb, *b*—*e*: c-treated bulbs.

opinion, many facts of interest. The expectations of BLAKESLEE and AVERY as to the value. for practical breeding work of the colchicine method have been fully confirmed in the present study. A great many facts go to prove that colchicine will constitute the agent long sought for, which, without detrimental secondary effects and with full certainty, induces polyploidy. From a practical point of view colchicine has many advantages over the methods hitherto prevalent for increasing the chromosome number. Of importance is, for instance, that the colchicine action is specific and total. No other disturbances besides the inactivation of the spindle apparatus are observed, at least if the c-exposure is not prolonged too much and the concentrations employed are not too strong. The completeness of the action of colchicine is remarkable. All the mitoses taking place within the exposed tissue turn into

c-mitoses and bring about chromosome doubling. Of importance is also the reversibility of the inactivation process of the spindle. After the conclusion of the exposure the spindle apparatus recovers and is able to function in the normal manner. Cells with increased chromosome number are thus brought back to normal mitoses after their period of rest.

The results of the present study refer exclusively to the root meristeme, where the chromosome conditions are easy to investigate, but probably there is no essential difference in the c-effect in other

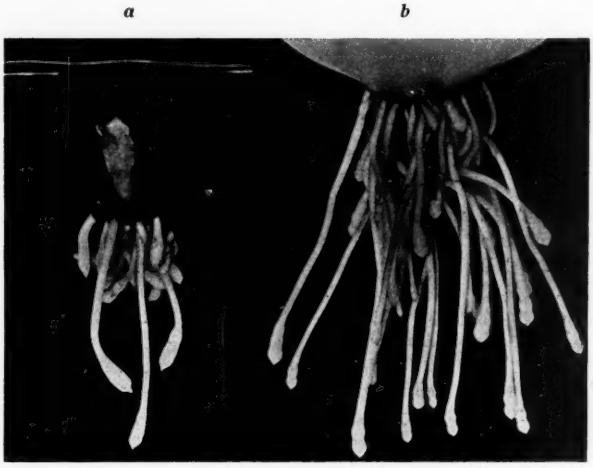


Fig. 7. The formation of colchicine tumours. *a*: bulb treated with 0,1 % colchicine for 8 days; the calyptra is clearly visible; *b*: colchicine treatment alternating with periods in pure water; the tumours take the shape of strings of pearls.

embryonic tissues. The root mosaic is characterised by the different elements being mixed at random, and no tendency could be found to the formation of whole sectors with changed chromosome number.

The possibility of macroscopically diagnosing colchicine-induced polyploidy may be of some practical use. As is seen from Figs. 6 and 7, tumours are formed by the root meristeme, while the length growth ceases altogether [compare control Fig. 6 *a* with c-treated bulbs (with 0,1 % colchicine for 5 days) Fig. 6 *b*—*e*]. As has already been emphasized, this phenomenon is caused by the increase in volume of the meristematic cells, while the formation of new cells is completely suppressed. An idea of the sensitivity of this macroscopic reaction may be had from

Fig. 7 *b*. This bulb has been treated with 0,5 % colchicine solution alternating with periods in pure water. The colchicine tumour then takes the shape of a string of pearls, each period in water being distinguishable as a constriction of the tumour. In Fig. 7 *a* the calyptra is very conspicuous; its meristeme contains fewer cells than the root meristeme and consequently it cannot swell to the same degree as the rest of the root tip.

Considering all the obvious advantages of colchicine for producing varieties with increased chromosome number, it seems very likely that colchicine, on account of its specific and infallible action, will be of great practical use and possibly take the place of the more whimsically acting agents for the production of polyploids hitherto in vogue.

LITERATURE CITED.

1. Blakeslee, A. F. and Avery, A. G. 1937. Methods of inducing doubling of chromosomes in plants. — Journ. of Hered. 28: 393—411.
2. Darlington, C. D. 1937. Recent advances in cytology. Second ed. — London.
3. Darlington, C. D. and Thomas, P. T. 1937. The breakdown of cell division in a *Festuca-Lolium* derivative. — Ann. of Bot., N. S. 1: 747—761.
4. Dixon, W. E. 1905. A manual of pharmacology. — London.
5. Dustin, A. P. 1934. Action de la colchicine sur le sarcome greffé, type Crocker, de la Souris. — Bull. Acad. R. Med. Belg. 14: 487—505.
6. Levan, A. 1936. Die Zytologie von *Allium Cepa* × *fistulosum*. — Hereditas XXI: 195—214.
7. Lits, F. J. 1934. Contributions à l'étude des réactions cellulaires provoquées par la colchicine. — C. R. Soc. Biol. 115: 1421—1423.
8. Ludford, R. J. 1936. The action of toxic substances upon the division of normal and malignant cells in vitro and in vivo. — Arch. f. exp. Zellf. 18: 411—441.
9. Nebel, B. R. and Ruttle, M. L. 1938. The cytological and genetical significance of colchicine. — Journ. of Hered. 29: 3—9.
10. Stein, Emmy. 1936. Die Doppelchromosomen im Blütenbezirk der durch Radiumbestrahlung erzeugten Mutante »cancroidea» von *Antirrhinum majus*. (Somatische Chromosomen-Reduktion). — Zschr. f. ind. Abst.- u. Vererbungslehre 72: 267—286.

NOTE ON HETEROPLOID TWIN PLANTS FROM ELEVEN GENERA

BY *ARNE MÜNTZING*
SVALÖF, SWEDEN

IN a previous paper, published in Cytologia (MÜNTZING, 1937), the present writer gave an account of chromosome numbers in twin seedlings of various plant species. This investigation was started especially on account of the results obtained by Japanese workers, who had observed individuals with widely deviating chromosome multiples among twin plants of wheat. In the report mentioned I was able to demonstrate that the occurrence of new polyploid forms among twin seedlings is not limited to the genus *Triticum*, twins with deviating chromosome numbers also being observed in species belonging to six other genera. These aberrant plants were briefly described, and their probable mode of origin considered (l. c., pp. 220—226). These considerations and the discussion of the theoretical and practical importance of the method were based on the twin material collected in 1935—1936. Since then, this material has been much enlarged, in 1937 and 1938, and therefore it may be appropriate to give a brief summary of the total results hitherto obtained. These data are summarized in Table 1.

As is evident from the table a total of 2201 twin plants have now been examined, and among them 95 individuals were found to have deviating chromosome numbers. This corresponds to an average percentage of $4{,}32 \pm 0{,}43$.

In the beginning of the work the chromosome numbers of all twin plants available were determined, but later on simplified methods were introduced. The first simplification undertaken is based on the fact that the twins with deviating chromosome numbers are almost exclusively found among the so-called *b*-plants, representing those members of the twin pairs which are weak at the seedling stage (l. c., pp. 221—222). Therefore, in the annual cereals only the *b*-plants are now cytologically examined. However, if an aberrant *b*-plant is found, the chromosome number of the corresponding *a*-twin will also be determined for the purposes of control. In all cases hitherto examined

this number was found to be normal. — In the perennial species the work is simplified by letting the entire twin material grow up in the experimental field. After a morphological inspection only those twin pairs are selected for cytological examination in which the members differ visibly in appearance. In the majority of the material the twins are morphologically identical and give the impression of being clone plants, resulting from vegetative division. It is probable that such

TABLE 1. *Results obtained by the twin method.*

Species	Number of twin plants examined	Observed number of				Percentage of plants with deviating chromosome numbers
		Triploids	Haploids	Tetraploids	Other deviations	
Triticum vulgare	426	18	1			4
» *turgidum*	6	2				(33)
Secale cereale.....	268	2		1		1
Avena sativa	262	23		1		9
Hordeum vulgare	93	1	2			3
Phleum pratense...	446	6	3			2
Dactylis glomerata	198		2			1
Festuca pratensis	34	1				3
» *rubra* ...	32	1				3
» *ovina* ...	6					(0)
Lolium perenne...	105	4				4
Agrostis stolonifera	31	1				3
Cynosurus cristatus	17					0
Poa pratensis	270	18	2		5	9
Trifolium pratense	3					(0)
Solanum tuberosum.....	4		1			(25)
Total	2201	77	11	2	5	$4{,}32 \pm 0{,}43$

identical twins result from the splitting of one original embryo. In other cases the twins are more or less different in morphology, and all such twin pairs have been cytologically examined. However, only part of them were found to differ in chromosome number. Thus, in cross fertilizing species such as *Phleum pratense* and *Dactylis glomerata,* there are three categories of twin pairs, *viz.* a) those in which the members are pheno- and genotypically identical, b) those in which the members are morphologically dissimilar but have the same, normal

chromosome number and, finally, c) those in which the members differ morphologically as well as in chromosome number. — A fourth, exceptional, category has been found twice in *Lolium*, both members of the pair having the same deviating chromosome number ($2n = 21$ instead of $2n = 14$).

Of these categories, the one consisting of identical twins is the largest. For instance, of the *Phleum pratense* twins grown in the experimental field last summer, 108 pairs and 2 triplets consisted of apparently identical members. In 43 other pairs morphological differences were observed. Some of these differences were probably due simply to environmental conditions, but in other cases the members must have been genotypically different. All these pairs were cytologically examined, but only four plants were found to have deviating chromosome numbers, three having 63 chromosomes instead of 42, the fourth plant being a haploid ($2n = 21$). — In *Dactylis glomerata* the members of 27 pairs and 1 triplet were found to be morphologically identical, whereas more or less conspicuous differences were observed in 12 pairs. Only one of these plants, however, was found to have an aberrant chromosome number, this individual being haploid ($2n = 14$). In the other genera studied there was a similar ratio between the apparently identical and the dissimilar twin pairs.

In general it was found to be relatively easy to identify haploids morphologically. In all the five genera in which haploids were observed they were rather conspicuous by their small dimensions. Triploids, *i. e.* individuals having a 50 per cent higher chromosome number than normal, could not be morphologically identified with certainty, and were only detected thanks to the slight quantitative difference observed in twin pairs containing such members. Since the morphological difference in such cases may be very slight, it is possible that some triploids may have been overlooked. Thus, the percentage values in Table 1 represent *minimum values*. However, the difference between the actual and the observed values is probably rather slight. This is evident from a comparison between Table 2 in my previous paper (MÜNTZING, 1937, p. 218) and the data now presented. According to the first table, the average percentage of deviating twins is $5{,}04 \pm 0{,}98$, the corresponding value of the second table being $4{,}32 \pm 0{,}43$. The difference is rather slight and not significant, though the first value is based on direct chromosome counts of all the twins, whereas the second value is mainly based on the simplified methods described above.

When comparing the two tables, it is striking that an enlargment

of the material has lead to the production of deviating twins also in genera in which no such twins were obtained at the first attempt. Thus, in the 1937 paper negative results were reported for *Hordeum vulgare, Dactylis glomerata, Festuca pratensis, Festuca rubra* and *Agrostis stolonifera.* After the enlargement of the material from 496 to 2201 individuals aberrant twins have now been found also in all these species. Thus, though comparatively laborious, this method is evidently of a rather general application. It is true that most of the species tested belong to the family *Gramineæ,* but a haploid twin was also observed in the genus *Solanum.* This haploid potato has been further studied by LAMM (1938). Twin seedlings also occur in apples, and in one case the twin members were found to have different chromosome numbers (BERGSTRÖM, 1938).

In contrast to other experimental methods of changing the chromosome number the twin method predominantly results in aberrants with odd chromosome multiples, triploids being most frequent. As may be seen from Table 1 not less than 77 of the 95 aberrants were triploids, in comparison with the normal chromosome number, these plants having 63 chromosomes in *Triticum vulgare, Avena sativa* and *Phleum pratense,* 21 chromosomes in rye, barley and *Festuca pratensis,* etc. — The haploids come next in frequency, a total of 11 haploids of 6 different species being obtained. The tetraploids, on the contrary, are quite rare and have only been observed once in rye and once in oats. Unfortunately both these tetraploids died before maturity. — In *Poa pratensis* the situation is complicated by the occurrence of apomixis and widely different chromosome numbers in different biotypes. Though most of the aberrants obtained in this species could be classified as triploids or haploids there remained some twin pairs, showing other deviations in chromosome number.

Though all species hitherto tested on a sufficiently wide scale have produced aberrant twins, it is evident that there are differences in the frequencies of such aberrants. In oats, for instance, 23 triploids and 1 tetraploid were obtained from 262 twins examined, the corresponding result in *Dactylis glomerata* being only 2 haploids from 198 twins. This gives the percentage values $9{,}16 \pm 1{,}78$ and $1{,}01 \pm 0{,}71$ respectively, these values being significantly different. The causes underlying such differences, as well as the entire mode of formation of the aberrant chromosome numbers, are at present unknown. Pending embryological investigations, we must at present be content with the fact that by raising twin seedlings a rich material of heteroploids may be obtained,

probably in most species of higher plants. Such heteroploids may be highly valuable both from the theoretical and practical point of view.

LITERATURE CITED.

1. BERGSTRÖM, I. 1938. Tetraploid apple seedlings obtained from the progeny of triploid varieties. — Hereditas XXIV, pp. 210—215.
2. LAMM, R. 1938. Notes on a haploid potato hybrid. — Hereditas XXIV, pp. 391—396.
3. MÜNTZING, A. 1937. Polyploidy from twin seedlings. — Cytologia, FUJII Jubilee Volume, pp. 211—227.

GENETICS IN RELATION TO GENERAL BIOLOGY

BY *ARNE MÜNTZING*
SVALÖF, SWEDEN

(*Inauguration Address delivered at Lund University on March 5th, 1938*)

THOUGH the science of genetics represents a well defined subject with its own specific problems, there are also several fields of research transitional between genetics and the other branches of natural science. On this occasion it may be appropriate to discuss some of them, in order to emphasize the connection between genetics and the other biological subjects.

I shall commence with the importance of genetics for taxonomy, in the first place botanical taxonomy but in principle also the zoological. The general qualification of biological classification is the occurrence of variation and discontinuity in nature. It is a well-known fact that both of these phenomena are highly characteristic of living organisms. The earth is full of living beings with the most variable appearance, but the borderlines between them are not continuous — on the contrary, they are more or less distinct. For that reason species and other taxonomical units may be distinguished.

From time immemorial the nature and causes of biological variation have been subject to speculation, but not until recently could the nature of this variation be clarified by the methods of experimental genetics. As is well-known, LAMARCK thought that variation was due to individual adaptations, which were transferred to the progeny and gradually fixed hereditarily. In the main DARWIN operated with the general occurrence of a spontaneous inherent and heritable variation directed by natural selection. DE VRIES, again, considered variation to be mainly due to mutations, *i. e.* sudden spontaneous changes of the genetic constitution. After the re-discovery of MENDEL's laws of heredity the science of genetics has been able to demonstrate that none of these older views was quite correct, but that variation comprises several quite different phenomena.

As is well-known from elementary text-books of genetics, two individuals may be different on account of purely environmental con-

ditions, every organism possessing a certain degree of adaptive plasticity. It may also be a question of genetic re-combination or, finally, of mutation, the mutations representing such a heritable variation as is not due to re-combination. This definition of a mutation is rather negative and is caused by the fact that the term has been found to cover several different phenomena. Firstly, it may be a question of real gene mutations, *i. e.* alteration of individual genes. It must be assumed that the genes consist of large, complicated molecules and that the mutation implies a minor change of the atomic arrangement in this molecule. This idea may seem to be an arbitrary speculation, but recently evidence has been obtained which demonstrates that at least part of the gene mutations are caused by intramolecular alterations. The comprehensive results obtained by the combined efforts of genetics and radiation-physics can scarcely be interpreted in any other way than that some gene mutations are really conditioned by usually reversible re-arrangements of the atoms in the gene molecule.

However, many mutations, spontaneous as well as induced, are certainly caused by more or less profound alterations of the chromosome structure, and there are probably continuous transitions between qualitative intramolecular changes and quantitative structural changes. It is true that the chromosomes possess a high degree of constancy, but it is now also known that their structure may sometimes be altered spontaneously or as a consequence of experimental influences. These structural alterations will often have external consequences, which are classified as mutations. — A third category of mutations, finally, is represented by alterations in chromosome number, comprising changes of the number of genomes or of individual chromosomes. Such alterations are now very well known, especially in the higher plants, but formerly they could not be dinstinguished from other types of mutations.

Thus, since 1900 genetics has been able to explain rather fully why organisms vary and what this variation really implies. Therefore, since variation is one of the basic postulates of taxonomy, it may be stated that in this field genetics has been of profound value to biological classification.

This is also true, perhaps to a still higher degree, with respect to genetic investigations of the causes of discontinuity in nature. The matter stands thus, indeed, that the species names of the taxonomists are not labels arbitrarily attached in order to survey a quite continuous variation. In nature there is indeed a real, though more

or less pronounced, discontinuity, the causes of which have to a certain extent been clarified by the results of genetics.

If we first consider the conditions within the species, we shall find that there is a universal differentiation in ecotypes, *i. e.* groups of biotypes corresponding to different habitats. In such cases discontinuity is due to the fact that the species population has been differentiated by natural selection, only such groups of biotypes surviving which are genetically specialized for different kinds of habitats. — Of greater importance from the systematical point of view is the comprehension of the limits surrounding the different plant and animal species. It has been known for quite a long time that, as a rule, different species are separated by barriers of incompatibility and sterility, *i. e.* if hybrids are formed at all they are more or less sterile and their eventual progeny more or less poor. — This is in itself a rather strange fact, though we have become accustomed to find it natural that the organisms are differentiated into separate species. In fact there might just as well prevail a complete continuity in the organic world. Thanks to the results of genetics, however, we can now understand fairly well why there are different species, and we also know a great deal about the barriers separating different species from each other. To begin with, it may be stated that these barriers are of several, essentially different kinds, and from this fact it is clear that in nature there are several quite different categories of species, which can hardly be brought together under a universal species definition.

The most common barrier between two species implies that the species cannot intercross, no fertilization taking place, or the hybrid embryo dying at a more or less early stage. The causes of such a condition may be quantitative as well as qualitative. Among the higher plants, for instance, difficulties of hybridization often occur when crosses are attempted between types representing different links in a polyploid series. This condition may be met with to the utmost extent also in crosses between an autotetraploid and its diploid original form. In such a case the parental types have only a quantitatively different constitution. However, a quantitative difference in chromosome number influences cell size, rate of cell division and other physiological properties, and this is probably the ultimate cause of the failure of such crosses. On the other hand, it is known that pollen tube growth may be highly influenced by specific genes in the pollen grains and stylar tissues. It is also known that quite small alterations in chromosome structure may have a similar effect. Thus, among the higher plants

the failure of a species cross may be due to relatively insignificant gene or structure differences between the parents. Finally, also plasmatic differences may affect the result of the cross.

As just mentioned, it is typical of species hybrids that they are more or less sterile. What is the cause of this sterility which may appear in several different types? The easiest to understand are the frequent cases in which meiosis in the hybrids is irregular. This irregularity may either be due to the fact that the species crossed have different chromosome numbers, or it may be caused by incomplete homology between the genomes of the parents. In both cases most of the gametes in the hybrid will die because they receive unbalanced chromosome complements. The hybrids may also be more or less sterile even if meiosis is apparently regular, and in such cases sterility is generally caused by the fact that by regular re-combination the gametes receive unsuitable combinations of the genes of the parent species.

Evidently, chromosomes and genes cannot be combined in just any way, but only certain definite constellations give viable gametes, individuals and species. Certainly, these constellations have to a great extent been fashioned by natural selection, the individuals possessing unsuitable gene combinations for the given habitat being eliminated. Thus, to a certain degree species differentiation is due to discontinuity of the environment. Another fact of importance, however, is that there is reason to assume the occurrence of purely internal conditions of balance between the genes. Only a limited number of combinations represent harmoniously co-operating systems, just as in the inorganic world atoms cannot unite arbitrarily, only a limited number of combinations representing stable chemical compounds.

Further, a very frequent cause of sterility in species hybrids is that the chromosomes differ in structure, the genes in the two species being arranged differently. This kind of sterility may also occur as a consequence of spontaneous intraspecific changes in chromosome structure. This being the case, there is reason to believe that the primary process in species differentiation is often the origin of such structurally conditioned sterility barriers, which split the original species population in two parts. On account of the barrier the two structure types will proceed to develop independently of each other, for instance, by gene mutations. This may easily lead to a combination of the sterility barrier with external differences, which are sufficiently marked to allow the two populations to be regarded as separate species.

Finally, I may call your attention to still another form of discontinuity, *viz.* the one occurring between different apomictic organisms. The loss of sexual propagation in the apomicts entails a strict constancy, facilitating the taxonomical description and naming of separate biotypes or small groups of biotypes. The question may be raised as to what extent genetics has contributed to an elucidation of the apomixis problem. — Originally these phenomena were exclusively studied by means of embryological methods, but more recently it has been possible to approach the problem more closely by combining embryology with cytological and genetical investigations. In this way it has been possible to analyse more closely the different forms of apomixis and further to detect several new apomictic species and genera, this throwing new light upon the taxonomy of the groups in question. So far we do not know for certain *how* apomictic organisms arise from sexual ones, but it seems probable that before long it will be possible to solve this problem by combined cyto-genetic and embryological efforts.

From the account and arguments discussed above it is evident that genetics has made important contributions to the analysis of variation and discontinuity in nature. These problems are of great general importance for taxonomy, but the question may be raised whether genetics is also able to aid taxonomy in the practical work of classification. This is undoubtedly the case, especially with respect to the so-called critical genera, which are impossible to analyse simply by morphological and phytogeographical methods. — The degree of constitutional similarity may be judged fairly well by crossing experiments. If the cross succeeds without difficulty and the hybrids obtained are quite fertile, the parents must be closely related and must be included in the same species. In the opposite case the parents are separated by more or less profound gene, structure or genome differences. Thus, by crossing experiments it is possible to clear up the barriers of incompatibility and sterility occurring in nature. This alone is of great value, since the species limits are generally and rightly drawn with the guidance of such barriers.

However, with the help of cytological methods of research it is possible to get much further. When comparing different taxonomical units, such a simple cytological task as the determination of the chromosome numbers may be quite valuable and allow certain conclusions to be drawn as to the relationship of the types compared. This is especially the case among higher plants, in which polyploidy is frequent.

If a certain species is found to be polyploid, the conclusion may be drawn that genotypically it is constituted either by a certain number of homologous genomes or by the genomes of two or several species with lower chromosome numbers. Which of these alternatives is the right one may generally be decided by studies of the chromosome pairing at meiosis. If more than two genomes are homologous this will generally lead to the formation of multivalent chromosome associations, only bivalents being formed in the opposite case.

For forming an estimate of the relationship between two species the mode of meiotic behaviour in their hybrids is quite important. Especially by studies of the degree and type of chromosome pairing rather detailed conclusions may be drawn as to the relationship of the species. This is especially the case when several species belonging to the same or closely related genera are crossed with each other in all directions. As a result of such a genome analysis each species will get a special letter formula, in which each letter corresponds to one genome. As is well known the wheat species with 14, 28 and 42 chromosomes are, for instance, designated by *AA*, *AABB* and *AABBCC* respectively. The diploid rye has another genome and the formula *DD*.

The cytological methods of research are not exhausted by the determination of the chromosome number and the investigations of the mode of meiosis. Since, at least in favourable material, the chromosomes have been found to have a more or less pronounced morphology, it is possible in species and hybrids to identify special individual chromosomes or chromosome categories. This chromosome morphology, which has developed into a special field of research, is of course of great importance for judging the constitution and relationship of different species. In favourable cases it may be established, for instance, that a species with a high chromosome number is constituted by the same chromosome types present in two other species with lower chromosome numbers.

The value of cyto-genetic methods of investigation for taxonomy is especially well illustrated by those cases in which it has been possible to synthesize experimentally species already existing in nature. In such cases it has been a matter of different links in a polyploid series, crosses between forms with low chromosome numbers giving rise to polyploid products. Both morphologically and cytologically these products have been found to be identical with already existing species. Thus, some time long ago these species must have arisen in nature in a similar way as now in the experiments.

One of the most elementary but also most fundamental theses of genetics states that the properties of the organisms result from a permanent interaction between the hereditary constitution and the environment. Therefore, every genotypical change implies a changed reaction norm, a new mode of reacting to environmental conditions. This being the case, it is natural that genetics has many points of contact with physiology and, indeed, it has been found to be of great interest to test the effect of hereditary alterations by physiological methods.

The most frequent type of hereditary variation is represented by genetic re-combination, which is mainly responsible for the enormous polymorphism which is generally characteristic of the different plant and animal species and also of man. This polymorphism does not only involve morphological differences but in a still higher degree it implies a physiological polymorphism. — From plant breeding work it is, for instance, well known that there may occur very marked genetic differences in properties such as winter hardiness, earliness and photoperiodicity, though these physiological differences are not at all correlated with any external characters. The same thing holds true of the resistance to various diseases, which is hereditary not only in plants but also in animals and in man.

When new hereditary factors arise by gene mutation, this will generally also have physiological consequences parallel to the morphological effects. In *Drosophila* it has even been possible to demonstrate that most of the mutations occurring are exclusively physiological. In a general way this may manifest itself as a changed viability, or it may have a more specific effect, for instance, a changed temperature optimum. Such a condition is of great interest with respect to the capability of a species to expand its area and to adapt itself to new ecological conditions. Thus, a physiological mutation may not be well adapted to the environment in which it arose but may flourish under other climatical conditions and cause an expansion of the distribution area of the species.

Exactly the same conditions are met with in the case of the genome mutations, *i. e.* changes in chromosome number leading to the origin of polyploid series. It has been observed that a doubling of the chromosome number does not only induce a series of characteristic morphological alterations but has also physiological consequences. Thus, for instance, the rate of cell division and the entire rhythm of development will be affected and also properties such as osmotic pressure, winter hardiness, vitamin contents and assimilation intensity.

Such physiological effects do not only accompany experimentally induced polyploidy but are also known from nature to play an important rôle in species formation.

As just pointed out, individuals, with all their detailed properties, are formed by an interaction between the genetic constitution and the environment. But what is the exact nature of this process? Why does a fertilized ovule develop in just the special way characteristic of the species in question?

There is now an important and active field of research, intermediate between genetics and physiology, working with these problems. In the main these questions have been studied in different insects, but during the last years the problem has also been attacked with the help of botanical objects. The main results hitherto achieved are the following: The individual development implies a series of accurately balanced reactions, which interact at definite times. These reactions are regulated by definite substances, »Wirkstoffe», which are possible to isolate chemically. Hitherto it has not been possible to determine the chemical constitution of these substances, but it is evident that they belong to the same main category as hormones and vitamins.

This field of research is especially based on GOLDSCHMIDT's investigations of intersexuality in *Lymantria.* During the last few years interesting results have also been obtained in other insects, especially in *Ephestia* and *Drosophila.* In *Drosophila,* for instance, the problem is attacked by means of transplantation experiments. In this material it is possible without difficulty to transplant eye-disks from one larva to the other and to get normal development of the transplants in the host. By moving eyes with a certain genotypical constitution to animals with other eye colour genes, it is possible to observe to what extent the transplanted eye is modified by substances present in the body fluid of the host. On the other hand, it is also possible to observe how the eyes of the host are influenced by substances produced by the implanted eye. By such experiments it has been possible to demonstrate the occurrence of three specific substances in *Drosophila,* which occur during definite intervals of time and in different concentrations in individuals with different eye colour genes.

Finally, to cite a case from the plant kingdom, there occur annual as well as biennial races of *Hyoscyamus niger*, this difference being caused by a single gene. However, by grafting shoots of an annual plant on a biennial one, it is possible to induce the latter to flower and thus change to annuality. This change has been found to be due to a

specific substance which, thanks to the grafting, can pass from the annual to the biennial tissues.

Scientists contemporary with MENDEL were of opinion that his results in *Pisum* represented special cases without much general importance. Thanks to the re-discovery of the Mendelian laws in 1900 and the work during the following years it became evident that MENDEL's results were of general validity. This was first demonstrated with respect to a series of different plant species and was soon also extendend to animals and finally to man. Already in 1905 FARABEE reported Mendelian inheritance of a finger defect in man.

It is now known with absolute certainty that the same laws of heredity are valid for all living organisms, uni- as well as multicellular, animals and plants as well as man. This holds true not only of the principle of segregation but also of several mendelistic complications such as linkage, polymerism, multiple allels, etc. — I should like to close this lecture with some examples, emphasizing this general validity of the laws of heredity. Let us commence with such a fundamental phenomenon as sexual differentiation and sex determination. It has been found that the 1 : 1 frequency, typical of the two sexes in man as well as most animals and several plant species, represents a back cross ratio due to the fact that one sex is heterozygous, the other homozygous. Corresponding to this genetical difference, there is a rather general occurrence of sex-determining *X* and *Y* chromosomes. Such chromosomes were first observed in a multitude of insect species. They have since been found in almost all groups of animals studied and finally also in man. Sex chromosomes, however, are not limited to the animal kingdom but have also been observed in many plant species. Thus, as regards the old question »male or female?», man is subject to exactly the same mechanism as, for instance, vinegar flies, dioecious mosses and several species among higher plants. This identity is not only true of the sex determination as such but also extends to the phenomenon of sex-linked inheritance. For that reason colour blindness in man is inherited in just the same typical way as, for instance, several eye colours in *Drosophila*.

As a second example of the general validity of the laws of heredity the death-conveying lethal factors may be mentioned. Among plants many cases of gametic lethals are known, which cause the death of certain definite categories among the sex cells. In animals and man, in which the life of the haplophases is shorter, only zygotic lethality is known with certainty, this lethality affecting the individuals them-

selves. These zygotic lethals are generally recessive and are only effective in a double dose. The lethal factors are not sharply distinguished from other genetic factors, and there are evidently continuous transitions between absolute lethals and the so-called sublethals, which have a less pronounced effect. In the same way there are transitions from the sublethal factors to such genes as affect vigour only slightly or not at all. — Concerning the real nature of the lethal factors it should be mentioned that at least some of them are now known to be deficiencies, involving quantitative structural chromosome alterations. This being the case, it is more correct to speak of factors than of genes with a lethal effect, since the term gene is generally used to denote a concrete unit of a chemical nature.

The most frequent lethals in plants are those inhibiting or disturbing chlorophyll formation. These factors may cause all graduations between normal and completely inhibited chlorophyll development. A multitude of other lethal and sublethal factors are also known from plant material, *e. g.* factors for poor endosperm development, for dwarfing and many other abnormalities. — In animals the classical case of lethality is represented by the factor for dominant yellow colour in mice, this factor being lethal in a double dose. It has been found that the homozygous yellow individuals are represented by demonstrable embryos, dying at an early stage of development. Thus, we have here a case of selective mortality before birth. Several other analogous cases have since been described, and in mouse, rat and swine about one third of the embryos die before birth. There is reason to believe that the early embryonic mortality is about equally comprehensive in man, and it is highly probable that this mortality is essentially due to lethal factors with a selective effect. In the same way the occurrence of a selective mortality among tender children has been demonstrated, the victims being individuals with a sublethal constitution.

Sometimes dog-day calves are described, which are in various ways monstrous and not viable. This is due to different specific lethals, which are rather frequent in cattle, in which they have been especially well observed on account of their economic importance. In such cases it is generally a question of factors allowing a more or less complete embryonic development, but which are followed by death at birth or shortly afterwards. Unfortunately, several analogous lethals are known in man, *e. g.* the factors causing Ichtyosis congenita, Xeroderma pigmentosum and one form of kidney cysts. To some extent it is possible to resign oneself to those lethals which act at an early stage, but it is

a more difficult matter with such hereditary diseases as juvenile amaurotic idiocy. Individuals happening to be homozygous for the factor in question have a normal child development, but at an age of about 10 years they are mercilessly killed after a period of physical and mental destruction.

A category of developmental disturbances in man, which challenge comparison with the conditions in certain plants, is represented by the different forms of heritable growth disturbances. As just mentioned, there is reason to assume a rather general occurrence of real lethal factors in man, which act at the embryonic stage. Several other factors are also known, which are not lethal, but which inhibit the growth of the body at a more or less early stage. Thus, there are at least four different forms of heritable dwarf growth, in which the inhibition sets in at a certain stage, either during the embryonic period or during childhood. The gradual series, represented by the different types of dwarfing, strikingly reminds one of essentially similar phenomena in a plant species. In maize a great number of factors are known, which when homozygous inhibit endosperm development at a more or less advanced stage. The strongest factors in this gradual series, *i. e.* those having the earliest action, have a lethal or sublethal effect, the seeds being poorly developed and not capable of germination.

After this discussion of the lethal factors in man and other organisms I would like to emphasize the great biological similarity between human populations and populations of cross fertilizing animals and plants. — In all closely studied plants and animals of this kind the populations may be said to be infected by large numbers of generally recessive factors, which consist either of real genes or of structural chromosome alterations. When homozygous these factors are responsible for certain morphological alterations, which are often more or less anomalous. Besides these factors with a morphological effect, which as a rule also influence viability, there is reason to assume a much greater category of factors having exclusively physiological effects and generally causing a decrease in vigour. Thanks to the cross fertilization all these factors occur in a heterozygous condition, and therefore viability is maintained. By inbreeding, on the other hand, a differentiation of the population material is produced, and at the same time the result is a more or less pronounced decrease in vigour. However, the results of the inbreeding are conditioned by the constitution of the starting material, and hence it is possible to produce, from the same

population, approximately homozygous inbred strains with quite different morphological properties and with all degrees of viability.

In man, in whom direct experimental results of this kind are not available, the direct evidence obtained is sufficient to demonstrate that, as regards inbreeding, man reacts in essentially the same way as all other cross fertilizers. Considering first the occurrence of factors decreasing viability, such factors are known in man by hundreds or even thousands. As is well known, these deleterious factors, either alone or in combination with each other, are responsible for a very large number of diseases and defects and are equally effective in the mental as in the physical sphere.

The study of human twins in particular has demonstrated that there are continuous transitions between genes with a strong and regular manifestation and cases in which there is only reason to speak of an inherited disposition for various maladies and defects. This heritable disposition is evidently much more important than was formerly supposed, and it can now even be stated that in most diseases there is probably a hereditary factor to be considered.

Thus, besides valuable, life-promoting genes human populations also comprise much heritable infirmity, which is conditioned by genetic factors having a more or less pronounced effect. Just as in the cross breeding animals and plants this frailty, especially as regards the recessive factors, is exposed by inter-marriage. If this inter-marriage proceeds to a sufficient degree the result will be an obvious differentiation of the population. This statement may be illustrated by the following well-known example regarding the populations of two small towns in New England. In both the towns there were only some 10 family names, a strong indication of inter-marriage and the close relationship between the inhabitants. In one of the towns the population was characterized by normal or even prominent intelligence and talents and by a good capability of productive work, this resulting in high prosperity. However, at the same time the people were often insane, and suicide was frequent enough to be considered almost as the normal end of life. — In the other town, on the contrary, most of the inhabitants were imbecile and their morals very primitive, especially in the sphere of sexuality. The people lacked desire as well as the ability to work, this resulting in general poverty and misery. — Thus, it is evident that in these towns inter-marriage had led to two relatively homozygous strains of different types, one of them being quite deficient. This result

is exactly comparable to the products obtained by experimental inbreeding of, for instance, a rye population.

From this example and the facts previously discussed it is clearly evident that the laws of heredity established in plants and animals are also completely and in part mercilessly valid in man. We are not allowed to observe at a distance how life in animals and plants is controlled by the rules of inheritance. On the contrary, this is evidently something that in the highest degree also concerns our own weal and woe. Therefore all problems of heredity in plants and animals acquire their deepest significance when viewed against the human background.

Having emphasized the general validity of the genetical laws, I should like to close this lecture by considering the problem exclusively from the human point of view. Thus, the question may be raised as to the main results hitherto obtained by human genetics. For the individual the most important conclusion is that his life and all his physical and mental properties are shaped by a continuous interaction between two, and only two, powerful forces: the inherited constitution and the environment in the broadest sense. — From the population and society point of view the most important result is the rather detailed knowledge of the numerous weak points in the human constitution acquired by the science of medical genetics. With this work a basis has been obtained for the measures aiming at an amelioration of the genetical constitution of the human populations. By continued work this basis will certainly become more and more reliable.

As is well known the practical application of genetics in the fields of plant and animal breeding has met with great success, while applied human genetics still remains in a preliminary stage. It is, indeed, extremely difficult to interfere in the composition of the human populations in a way that is both correct and effective. Knowing how much is at stake, it is evident, however, that no measures undertaken in a country can be of a greater importance than those which aim at a well-founded practical application on man of the results obtained by the science of genetics. The rapid progress of medical genetics nowadays seems to promise that it will some day be possible by human interference to control to a certain extent the laws of heredity governing ourselves as well as all other living beings.

Science
Library

76

JUN 13 1938

HEREDITAS

GENETISKT ARKIV

UTGIVET AV MENDELSKA SÄLLSKAPET I LUND

REDAKTÖR: ROBERT LARSSON

BAND XXIV HÄFT. 4

LUND 1938, BERLINGSKA BOKTRYCKERIET

HEREDITAS,

a periodical devoted to the publication of original research in heredity, is published by the MENDELIAN SOCIETY at Lund, Sweden. All contributions are written in English, German or French, illustrated, when necessary, with adequate text figures and plates. Each volume contains about 500 pages, issued in four numbers.

Subscriptions should be sent to the Editor. Price *Twenty (20) Swedish Kronor per volume.* Post free. (The price of Vols. I—X is 10 Swedish Kronor per volume, and of Vols. XI—XXIII, 15 Swedish Kronor.)

ROBERT LARSSON
Editor of »Hereditas»
3 Adelgatan, LUND, SWEDEN.

REDAKTIONSKOMMITTÉ

PROFESSOR, FIL. & MED. DR. *H. NILSSON-EHLE*
PROFESSOR, MED. DR. *HERMAN LUNDBORG*
PROFESSOR, FIL. DR. *HERIBERT NILSSON*
FIL. DR. *GUSTAV THULIN*

TILL MEDARBETARNA.

Manuskript — helst *maskinskrivna* — torde insändas till Redaktionen (Adelgatan 3, Lund) i fullt tryckfärdigt skick. De böra vara *noga genomsedda* för undvikande av ändringar mot manuskriptet. Obs. kommateringen! Korrektionskostnaderna betalas av författaren. Korrektur ställes till Redaktionen. Direkt förbindelse mellan författaren och tryckeriet tillåtes icke.

Personnamn sättas med KAPITÄLER. De markeras i manuskriptet med en våglinje. Latinska namn på växter och djur samt ord och satser av särskild vikt *kursiveras* (enkel understrykning).

Figurer numreras med arabiska siffror. Figurförklaring (på avhandlingens språk) torde insändas *samtidigt* med illustrationsmaterialet.

Planscher numreras med romerska siffror och de i dem ingående bilderna med arabiska.

Tabeller åsättas arabiska siffror och förses med kort rubrik.

Citerade arbeten samlas i en litteraturförteckning. I texten hänvisas till denna genom angivande av författare och årtal. Har en författare utgivit flera publikationer under samma år, tilläggas efter årtalet små bokstäver (a, b, c, etc.). Samma beteckningssätt användes i litteraturlistan, vilken uppställes i alfabetisk ordning efter författarna och under dessa i kronologisk följd. Inga litteraturhänvisningar få göras genom fotnoter. Överhuvudtaget så få noter som möjligt!

Avhandlingarna skola vara skrivna på tyska, engelska eller franska. Det är önskvärt, att uppsatser på tyska och franska åtföljas av en resumé på engelska. Översättningar, som ombesörjas av Redaktionen, bekostas av författaren.

Åt varje författare lämnas 100 fria separat. Avhandlingar på ett ark och däröver förses gratis med särskilt omslag. Till ett pris av 10 kr. pr 100 st. lämnas, om så önskas, omslag till mindre uppsatser. Större antal särtryck fås till självkostnadspris. *Anteckning om eventuella extraseparat göres å första korrekturet.*

INNEHÅLL.

Sid.

FEDERLEY, HARRY, Chromosomenzahlen finnländischer Lepidopteren I. Rhopalocera 397

BONNIER, GERT, Inherited Sex-Mosaic in Man and the Statistical Treatment of Such Data. An Answer to Professor S. G. LEVIT 465

LEVAN, ALBERT, The Effect of Colchicine on Root Mitoses in *Allium*..... 471

MÜNTZING, ARNE, Note on Heteroploid Twin Plants from Eleven Genera 487

— —, Genetics in Relation to General Biology 492

Seventh International Congress of Genetics.

In accordance with a resolution of the International Committee and with the decision of the Organising Committee elected by the Genetical Society of Great Britain, the VIIth INTERNATIONAL CONGRESS OF GENETICS will meet in Edinburgh in 1939, probably from August 23rd—30th inclusive. Professor F. A. E. CREW, Institute of Animal Genetics, University of Edinburgh, Edinburgh, 9, has been appointed General Secretary to the Congress and to him all correspondence concerning it should be addressed.

Utgivet den 25 maj 1938.